THE UNIVERSITY OF ALBERTA

TERRITORY AND TERRITORIAL BEHAVIOR OF MALE RUFFED GROUSE IN SOUTHWESTERN ALBERTA

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Territory and Territorial Behavior of Male Ruffed Grouse in Southwestern Alberta" submitted by Allan Edward Aubin in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The territories and territorial behavior of male ruffed grouse (*Bonasa umbellus*) were studied in southwestern Alberta during the spring, summer, and fall of 1969. Nine different territorial males were under observation for a total of approximately 100 hr.

Behavioral patterns involved in establishing and maintaining a territory were readily divisible into three components: (1) Restriction of all activities to a clearly defined space. This included courting females and fighting with, or pursuing other males, and performance of routine activities such as feeding, dusting, and sleeping. (2) Defense of that space. This was accomplished mainly through the use of threat behavior; either drumming or, rarely, actual fighting. (3) Advertisement from the space. This consisted of audibly advertising occupancy of a territory by drumming.

Courtship and threat displays were similar. Consummatory behavior (attack or mating) was released in the territorial male through the behavior of the intruder. Antagonistic displays were based on the erection and presentation of various feather groups, notably the ruffs and tail. These feathers were accentuated by their movements in display.

An analysis of dispersion of territorial males suggested that ruffed grouse are a non-lek species, in that males

live and display alone.

Territories were primarily mating areas and indicated that the function of territory should be regarded as behavioral phenomenon, rather than a spatial or geographic one in ruffed grouse.

Drumming logs were the focal point for territorial activities of the males in spring. The pattern of use of areas near the logs varied daily and seasonally. Daily, 2 periods of concentrated use near the logs were seen: in the early morning, and late afternoon. As the breeding season waned, after mid-May, a lesser absolute amount of time was spent near the logs.

Minimum sized territories of about 1.0 acre were established and maintained; they did not appear to overlap.

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1. INTRODUCTION

The nature of territory, and territorial behavior, of male ruffed grouse (*Bonasa umbellus*) were studied in southwestern Alberta in the spring, summer, and fall of 1969.

Territorialism in avian populations has received considerable recent study (Carpenter, 1958; Hinde, 1956; others). Establishment and maintenance of territory involves: restriction of some or all activities to a defined space, and defence of, and advertisement from, that space (Hinde, 1956). Since this behavior is most common during the reproductive season, studies of territorialism usually include an analysis of the courtship displays.

Territorial behavior has been well described in the tetraonids (Hjorth, 1967; Lumsden, 1961; MacDonald, 1968; Watson and Jenkins, 1964; others). However, less is known about how these displays relate to the biology of the species or to the relations among adjacent, territorial birds. This is particularily true in the grouse that display alone; the non-lek species.

There are two main views regarding the nature of territory in bird populations. One stresses that it is a behavioral phenomenon, rather than a spatial one (Carpenter, 1958). The other view holds that it is primarily an ecological phenomenon, important in partitioning the available habitat (Pitelka, 1959). It would seem that territorialism includes

both behavioral and spatial properties, although the benefits derived from a territorial system could be primarily spatial, for example, as ensuring an undisputed use of a food supply; or primarily behavioral, for example, as an aid in bringing the sexes together for mating. The various definitions of territory illustrate the lack of general agreement as to its biological significance (Lack, 1966).

Weeden (1965) discussed how a quantitative study of territory would provide some understanding of its functions, and give some indication of the behavioral systems involved. Two approaches to a study of territory could be made. In one the space utilized by the bird on a daily or seasonal basis could be studied. This would indicate any changes in the spaces utilized during the reproductive season. In the other approach, a study of the activity of individual members of the species could be made. This would indicate the use of the areas inhabited and the nature of the behavior involved. Both approaches need to be taken in order to provide a full understanding of the territorial system.

The term territory has often been applied to any space defined by a solid line connecting outer points of sightings of birds regardless of the time interval involved between sightings, the stage of the breeding cycle, or type of observation. Commonly, territory has been defined as any defended area (Noble, 1939), but if temporal changes in patterns and type of use of a space can be demonstrated, then it would appear more realistic to define the activity, including

defence, by a bird in a clearly defined time interval, and the space used concomitantly.

In the present study, a quantitative analysis of territorialism of ruffed grouse was made. Briefly, male ruffed grouse select elevated sites, usually fallen logs, from which to perform a drumming display. The display consists of a series of wing-beats made by the male, and results in the production of a number of dull thumps, the drumming sound. More than one drumming site may be selected, and these are distributed over an area termed the *activity center* (Gullion, 1967). Whether or not ruffed grouse defend an area near their logs (a territory) is unknown; some workers (Palmer, 1963; Sumanik, 1966) use the term without definition, while others avoid the use of the term (Fowle, 1953; Gullion, 1967). In the present study the term territory will be considered to represent a defended space.

Information about the antagonistic displays (reproductive and aggressive) of male ruffed grouse in nature are almost completely lacking, and these were also studied. Changes in behavior and spaces utilized by individual males were analyzed in relation to the stages of the breeding season.

2. DESCRIPTION OF THE STUDY AREAS

The same three study areas, the East, West, and Northwest, as described in Sumanik (1966), were used in the present study (Fig. 1). These are located in the Sheep River Valley of the Bow River Forest Reserve near the R. B. Miller Biological Station. The station is about 20 mi west of Turner Valley, Alberta.

Briefly, two major plant associations occur on the study areas: a closed-forest, climatic climax dominated by white spruce (*Picea glauca*), and a grassland topographic climax dominated by rough fescue (*Festuca scabrella*). Various seres of the climatic climax are represented on the areas: trembling aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*) seres. In the East Area, the forest cover is dominated by poplar (mainly trembling aspen, but with some balsam poplar (*P. balsamifera*)). Forest cover is incomplete, broken by open grassy slopes and benches, and ravines. By contrast, the West and Northwest Areas have a nearly complete forest cover, with white spruce and lodgepole pine found in pure stands or intermixed with poplar. In spite of these differences, male ruffed grouse used drumming logs mainly in mixed wood of spruce and poplar in all three areas (Sumanik, 1966). Two areas where observations of male ruffed grouse were made in the present study are shown in Fig. 2.

Fig. 1. Location of study areas in southwestern Alberta.

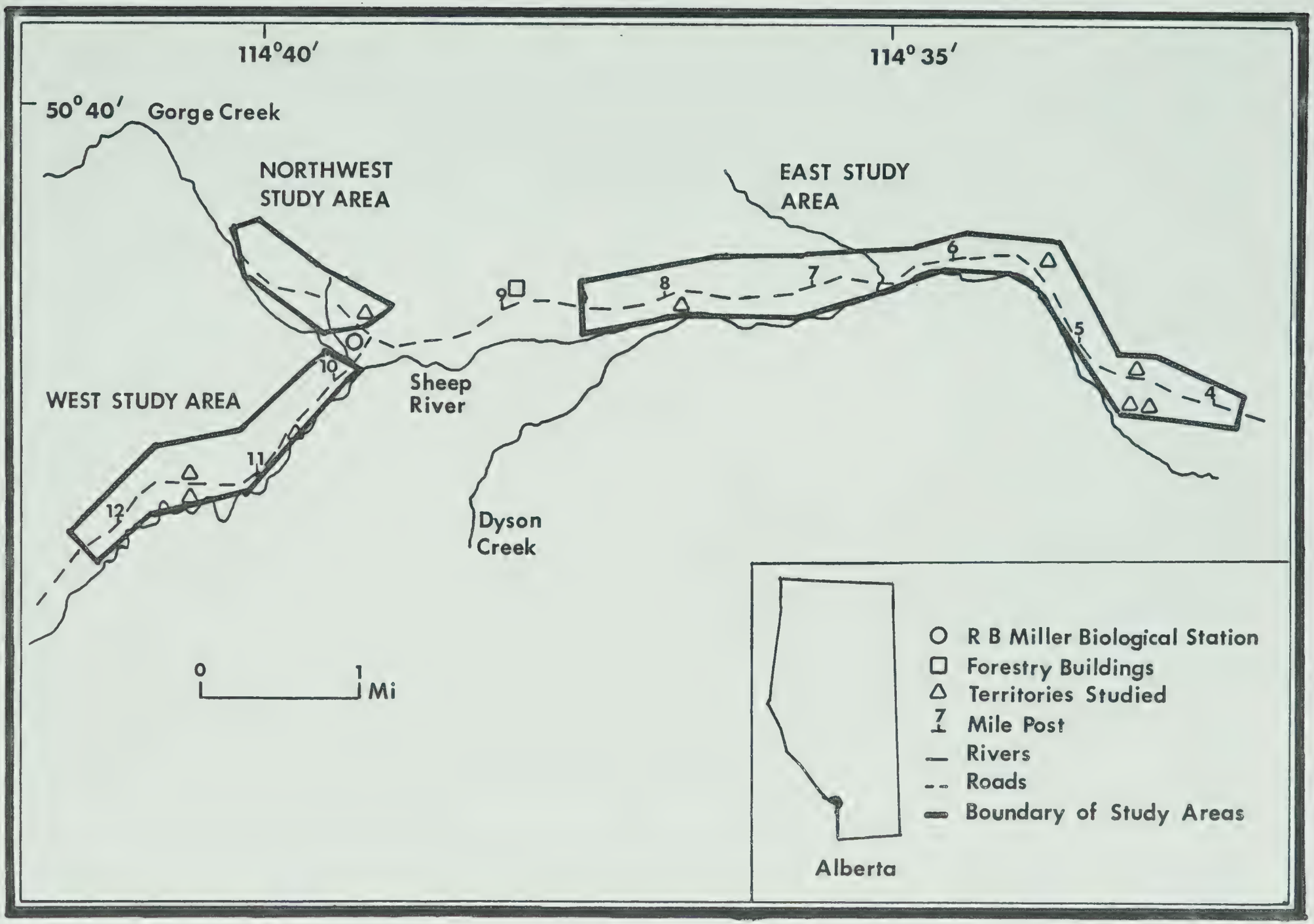
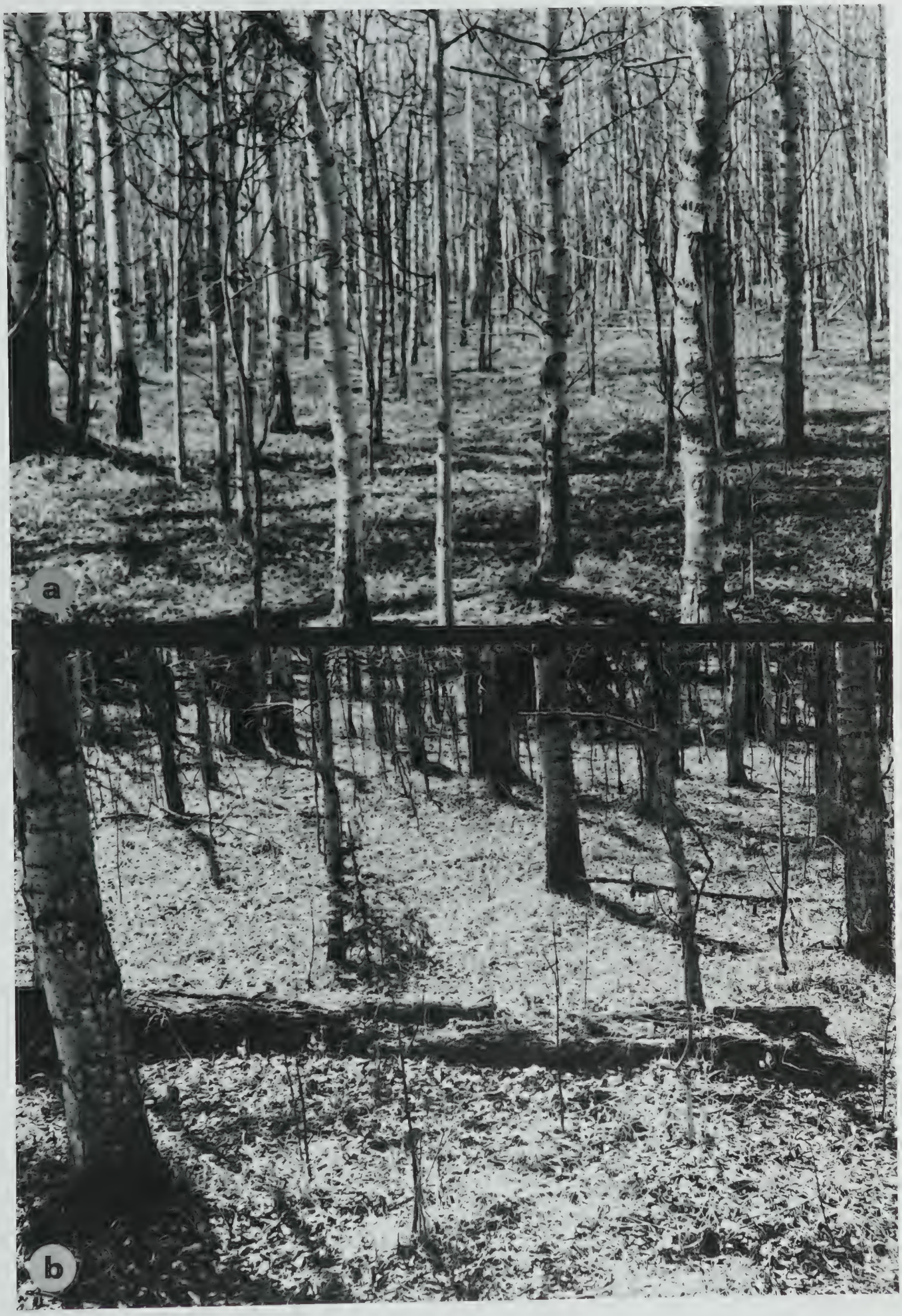

114°40′
114° 35′
50° 40′
Gorge Creek
NORTHWEST STUDY AREA
EAST STUDY AREA
WEST STUDY AREA
Sheep River
Dyson Creek
0
1
Mi
Alberta
R B Miller Biological Station
Forestry Buildings
Territories Studied
Mile Post
Rivers
Roads
Boundary of Study Areas

Fig. 2. Typical habitat within two different territories studied (East Study Area) in 1969. Note sparse understory in each and the drumming log in "b".


a
b

3. HISTORY OF PAST RESEARCH

Research on ruffed grouse in the vicinity of the Biological Station was begun in 1959 (Lewin, 1959). In this work ruffed grouse were shot indiscriminately in the area from 1959 to 1963. An analysis of the crop contents and reproductive processes were made. Evans (1961) spent one season studying the reproductive behavior of ruffed grouse in the same area.

The first systematic studies were begun in 1964 (Sumanik, 1966). This research was concerned with a vegetative analysis of drumming sites and with the effects of biotic and abiotic factors on drumming activity. At that time study areas were delimited and drumming sites were located, marked, and mapped. Since then an annual census of the male population in the East and West Areas (1966-1969) and in the Northwest Area (1969) has been conducted. Drumming males have been routinely captured and banded, and new drumming sites marked and mapped (Boag and Kiceniuk, 1966, 1967; Ewaschuk, 1968; present study, 1969).

In 1965 all drumming males in the West and Northwest Areas were removed (Sumanik, 1966). All males were not removed from the East Area, but each year an undetermined number of grouse are taken by hunters in all three areas. The numbers of males banded and the number of drumming sites used each year (1966-1969) in the East and West Areas

are shown in Table 1.

Table 1. Number of drumming male ruffed grouse on the East and West Study Areas, 1966-1969. Total number of marked birds present each year is also shown.

Study area (size in acres)*	Number of drumming sites occupied:				Number of marked** birds:			
	1966	1967	1968	1969	1966	1967	1968	1969
East (962)	7	10	23	18	4	9	10	11
West (608)	17	28	41	36	10	9	23	20

* Sumanik (1966)
** Including those that survived from previous years.

These data show that the male segment of the population has increased since 1966, "peaked" in 1968, and declined slightly in 1969 in both areas. The table shows the trend in numbers of birds and the population level at which the present study was begun.

4. METHODS

4.1 General

Behavior and activity of male ruffed grouse were studied by both observational and experimental methods. The study was begun in late April, 1969, and was concluded at the beginning of October of the same year. In addition, unpublished data in the files of the R. B. Miller Biological Station (1966-1969) obtained from previous studies in the same areas were analyzed. Techniques used in the present study included: 1) observations of drumming males; 2) estimation of population size and seasonal use of territories; 3) experimental test of the functions of drumming; 4) recording and analyzing the drumming sounds; 5) collection of ruffed grouse.

4.2 Terminology

Components of the habitat utilized by territorial male ruffed grouse are listed and defined for convenience. Definitions are given according to each authors' particular use. Some of the terms are ill-defined and are discussed later in this paper.

Drumming log---fallen trees, boulders, mounds of dirt, or other elevated objects; used to support the drumming male (Gullion, 1967).

Drumming stage-actual spot on the log where the bird drums (Gullion, 1967); synonomous with Sumanik's (1966) *platform*.

Drumming site---drumming log(s) and immediate environs (Gullion, 1967). Used to designate the vegetative characteristics around the drumming stage(s).

Primary log-----log used most persistantly for drumming by one male in a given season (Gullion, 1967).

Alternate log---log receiving some use but less than the primary log by the same male as above in one season (Gullion, 1967).

Activity center-the general forest area used by a male grouse which is associated with a specific log(s) and including 10 to 30 acres (Gullion, 1967). Apparently eqivalent to *home range*.

Territory-------area used by male ruffed grouse (apparently) in spring (Palmer, 1963; others). Area bounded by a number of drumming logs used by one male (Sumanik, 1966). Used in the present paper to designate the area used by a drumming male grouse in spring.

Primary areas---area used by drumming male grouse in spring (Fowle, 1953).

4.3 Observations

Daily observations of grouse were made from 2 blinds from 27 April to mid-June, 1969, and every third day from mid-June until mid-September. Observations were made from about 0330 to 0800 hr MST. Additional observations were made at various times in the day to 2000 hr. Both blinds were placed about 25 ft from the primary log of males observed. The behavior of each male, and the number of drumming sounds made by adjacent males were recorded. Repeated observations of

particular males were possible since a number of males had been banded previously. Each male was individually marked with a specific combination of colored and numbered aluminum leg bands. With one exception, only marked birds were studied from the blinds; in this paper, birds are refered to by their leg band number.

Temperatures were recorded to the nearest degree immediately before and after an observation period. Wind variations were estimated as light (<5 mph), moderate (>5<10 mph), or strong (>10 mph); and precipitation was recorded as light, moderate, or heavy.

One blind was left south of mile 4.5 in the East Area (Fig. 1) for the duration of the study in order to monitor continually the behavior of one male and the activity of adjacent birds. The second blind was periodically moved to drumming logs of other males to gather comparative data. In all areas adjacent drumming males were located by searching for them.

In most areas strips of surveyor's tape were tied to trees to provide a grid system covering the area of visibility from the blind. The locations of these were accurately measured with tape and compass relative to the blind site. The location of the blind, drumming logs and grid markers were plotted on data sheets (Appendix 1). Copies of these data sheets were used to map the activities of ruffed grouse seen in each particular area. These data sheets are known as field maps.

Mounted male and female ruffed grouse, and mirrors were presented to territorial males. In addition, a phonographic record of the drumming sound was played near the logs of some males in a further attempt to elicite responses. Behavioral data were recorded by taking notes, and by taking photographs with a cine' 8 mm Bell and Howell movie camera and a still 35 mm Miranda "G" single-lens-reflex camera.

4.4 Population Estimate and Seasonal Activity

A transect along which drumming sounds were counted, previously established in the study areas (Sumanik, 1966), was traversed daily from 27 April to 9 May, 1969, to estimate population size and to document spring drumming activity. The transect consisted of making 13, 4-min stops at approximately 1/2 mi intervals along the Forestry Reserve Road (Fig. 1) from mile 4.5 to mile 12.5. At each stop the number of drumming sounds heard, and the number of males making them were recorded. The transect was run every third day from July to September inclusive to determine the initiation and level of fall drumming activity. Transect runs were made between 0500 to 0700 hr.

The drumming logs of 30 banded males were checked weekly, from mid-June until mid-September, for fecal droppings presumed to have been left by the resident bird. These data gave some additional indication of the seasonal use of territories.

One or more chicks from 15 different broods were either

caught by hand or in a butterfly net and their ages estimated by the status of the replacement of post-juvenal primaries (Bump et al., 1947). From this sample of chicks the onset of laying and peak of hatch were estimated. Information about the initiation and duration of the post-breeding molt was obtained from yearling and adult grouse captured or shot.

4.5 Recording Techniques

Taped recordings of drumming sounds of all males studied were made with a Nagra III B tape recorder equipped with an "Electrovoice" cardioid microphone (Model 666) without reflector. The microphone was placed about 5 ft in front of the drumming stage and camouflaged with spruce branches. The cut ends of the branches were pushed into the ground around the microphone, completely hiding it from view. Care was taken to prevent the branches from touching the microphone. The lead from microphone to recorder was covered with leaves.

Four to 6 complete drumming sequences were recorded from each male. A foam wind-screen was always used on the microphone and, if the recordings were made in light rain or snow, a rubber prophylactic was first stretched over the microphone before the wind-screen was added. Sounds were recorded at a tape speed of 15 inches per second, with an input volume of 0 to -2 decibels.

To analyze the sounds the tapes were played at the same speed at which they were recorded. The signals were led into an "Intensity Meter" (Frokjer-Jensen Co., Germany)

and adjusted with an input volume of either 8 or 12 decibels. The meter was connected directly to a "mingograf 34" chart recorder (Elma-Schonander Co., Sweden) which printed out the amplitude of the signal as a function of time. The chart speed was set at 5 cm per sec which allowed all the components of the signal to be identified.

4.6 Experimental Test of the Functions of Drumming

A territorial male (No. 901) was removed from its territory and 4 modified lily-pad traps (Gullion, 1965) with connecting leads of wire-mesh were placed around the primary log. An area of about 1/3 acres was enclosed with the drumming log in the center. Near the log a taped recording of the drumming sound was played on the Nagra recorder from a continuous loop spool (Philips CE 10). The sound was amplified through a 24-volt transistorized amplifier (Philips EL6623) driven by 2 car batteries connected in series. The sound was played through a base speaker. The recorder, amplifier, and car batteries were enclosed together, and the speaker separately, in waterproof wooden boxes. The volume of the sound was adjusted so that it could be heard for up to 1/2 mi on a clear, windless day. The recording was played continuously at the rate of one complete drumming sequence every 3.3 min, for up to 12 hr at one time, every second day from 2 to 8 May, 1969.

The numbers, times of capture, sexes, and ages of all

grouse caught were determined. These were individually color-marked and released. The experiment was carried out immediately north of the Biological Station (Fig. 1). On 9 May the amplifier was destroyed by fire; consequently no further drumming was played from the area. However, the trap cells and leads were left operational until 27 September and provided some additional captures of grouse.

4.7 Collection of Ruffed Grouse

Throughout September, 1969, ruffed grouse were shot in the vicinity of the Biological Station. Some males were removed from the Northwest area, but none from the East and West Areas. A histological analysis of the testes was made to compare to a spring and summer sample collected previously in the same general area (collection of V. Lewin, Department of Zoology, University of Alberta). This analysis provided information about the basis of drumming activity in fall.

Testes of ruffed grouse collected in 1969 were treated similarily to Lewin's sample. Testes were removed within 5 min of the death of the birds and fixed for a two week period in Bouin's solution. The lengths and widths of each pair of testes were measured with vernier calipers to the nearest 0.1 mm, then stored in 70% ethyl alcohol. Testes were then embedded in paraffin and sectioned longitudinally at 7 microns, then stained with haematoxylin and eosin.

4.8 Statistical Methods

Appropriate statistical tests were taken from various sources, and references for these tests are given when the test is used. Differences at the 5% level of probability are considered statistically significant.

5. SEASONAL ACTIVITIES

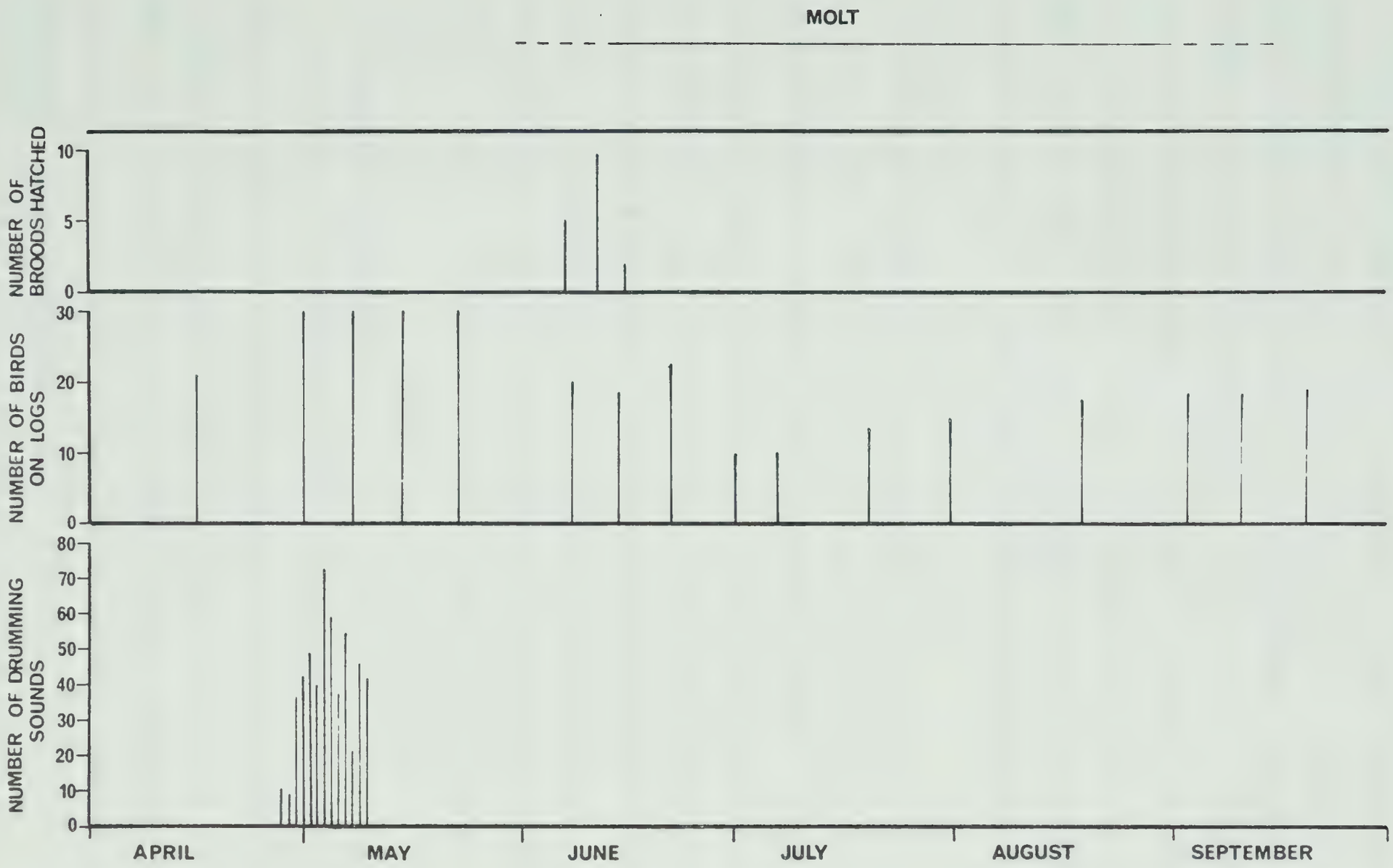
5.1 Attendance of Ruffed Grouse on Logs

Drumming logs of male ruffed grouse appear to be the focal point of their year-long activities (Eng, 1959). In spring and fall males have been reported to use an area near their logs of about 1.0 and 3.5 acres respectively, while in summer and winter the areas utilized are increased to between 4.0 and 10.0 acres (Eng, 1959; Fowle, 1953). Actual presence on the logs may occur at any time of the year, but the greatest proportion of birds use drumming logs in spring (Bump et al., 1947). In addition, my observations indicate that, at least from spring to fall, the time spent on drumming logs is maximal in spring.

The number of birds (sample of 30) using drumming logs from spring to fall, 1969, is shown in Fig. 3. For comparison, the number of drumming sounds heard along the transect each day from 27 April to 9 May, 1969, are included. The number of broods hatched per week over 3 weeks in 1969 is also shown. The extent, but not the number, of birds molting (post-breeding) is indicated.

Data on log attendance were obtained by checking a sample of drumming logs for the presence or absence of fresh fecal droppings.

Fig. 3. Summary of selected activities of ruffed grouse on the East and West Study Areas from April to September, 1969.


MOLT
NUMBER OF BROODS HATCHED
10
5
0
NUMBER OF BIRDS ON LOGS
30
20
10
0
NUMBER OF DRUMMING SOUNDS
80
70
60
50
40
30
20
10
0
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER

Logs were checked once in mid-April and at approximately weekly intervals from the first of May to mid-September, 1969. From the onset until the end of spring drumming activity, as determined from transect runs, log attendance was high (75-100%). Attendance fell off in June, coinciding closely with the initiation of the molt. In early July attendance began to increase. Logs were last checked on 21 September at which time 60% of the logs used in early spring were again being used.

The coincidence of the initiation of the molt and the decrease in log attendance are probably not directly related, but both may be associated with a general gonadal regression (see below). Increasing attendance from July to September might reflect a gonadal resurgence. Eng (1959) hypothesized that one of the proximate factors influencing drumming activity in the fall (and hence log attendance) may be defence of territory by adult males in response to an influx of sexually active juvenile males attempting to take up territories.

5.2 Drumming Activity

The number of drumming sounds heard along the road-side transect in 1969 indicates that drumming activity was low in early spring, reached a peak on 4 May, and ceased in early June. No drumming sounds were heard in July and August, but from mid-September until the end of the month, some drumming was heard almost every day.

Each day in spring, drumming began at between 0200-0300 hr. Activity reached a peak between 0400 and 0500 hr, then declined to a low level. The low level of activity was maintained throughout the day, then increased to reach a second, smaller peak at about 1700 hr. A representative pattern of daily drumming activity is shown in Fig. 4. This pattern of daily activity has been reported previously in ruffed grouse (Petraborg et al., 1953; Sumanik, 1966). In the present study no drumming was heard between 2000 hr and 0230 hr although no systematic attempts at recording sounds were made. Petraborg et al. (1953) report that during high populations of birds, drumming may occur sporadically during the night.

In contrast to spring activity, drumming was only heard in September from between 1000 and 1200 hr. Of 11 cocks shot in September, 10 were taken on drumming logs. Nine of these 10 were shot between 1000 and 1200 hr although birds were hunted throughout the day from about 0500 hr. These data indicate that the pattern of daily activity may vary between spring and fall. Also, activity in the fall was at a much lower level, and more sporadic than activity in the spring.

Drumming activity is undoubtebly influenced by both intrinsic and extrinsic factors. Drumming count data obtained over the past 5 years on the same study areas show that the peak of activity occurred on 3 or 4 May of each year, with one exception (Fig. 5). The data represent the total number of sounds heard each day along the transect. In 1967, the entire study area was blanketed by approximately 2 ft of snow

Fig. 4. Daily pattern of drumming activity determined from hourly counts of the drumming sounds at one listening stop, mile 11, West Study Area, on 7 May, 1968.

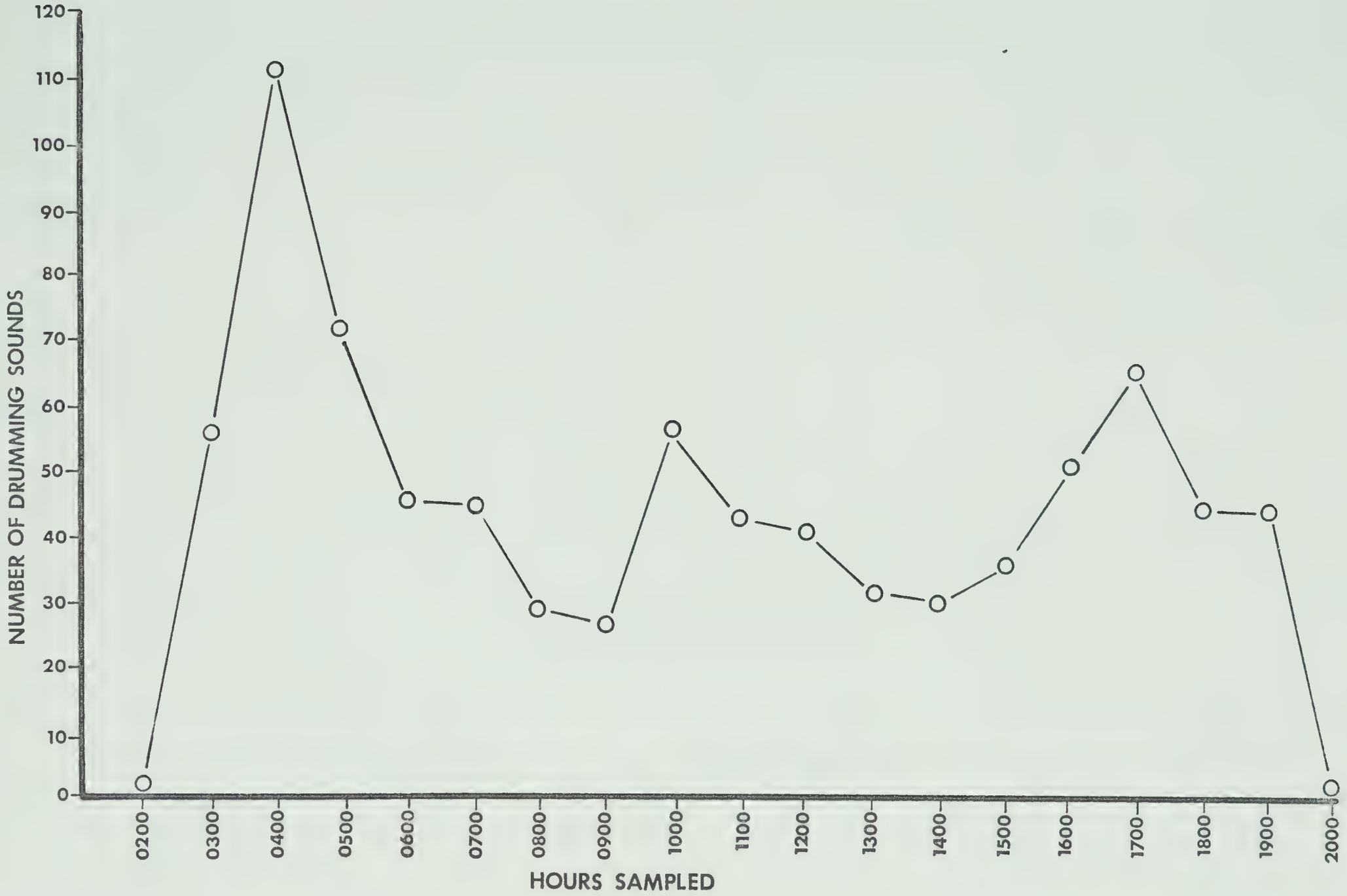
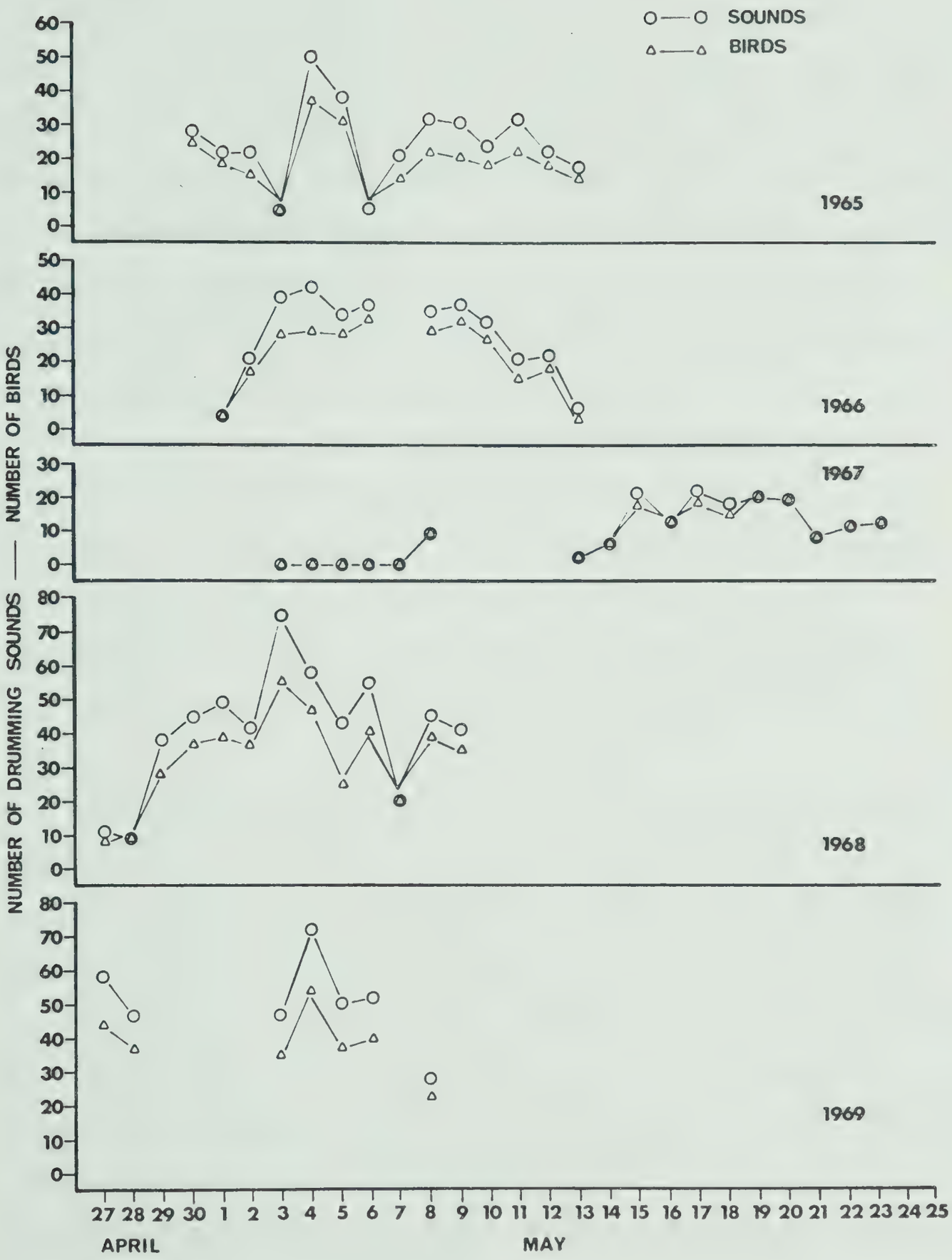

NUMBER OF DRUMMING SOUNDS
120
110
100
90
80
70
60
50
40
30
20
10
0
0200
0300
0400
0500
0600
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
2000
HOURS SAMPLED

Fig. 5. The total number of drumming sounds and the birds producing them, heard daily at 13, 4-minute-listening stops along an established transect (mile 4.5 to mile 12.5 Forestry Reserve Road) in the springs of 1965 to 1969.


SOUNDS
BIRDS
1965
1966
1967
1968
1969
NUMBER OF DRUMMING SOUNDS —— NUMBER OF BIRDS
APRIL
MAY

until 7 May. This appeared to be responsible for delaying the peak of drumming until 17 May---even then the activity was at a much lower level than is normally seen at the peak. Thus, with one exception, the drumming peak appears to be precisely fixed in time. Brander (1967) reported that a peak in drumming occurred during a short and well-defined time interval over a period of years for an eastern population of ruffed grouse. These data suggest that the factors influencing drumming are also fixed in time.

Available evidence suggests that photoperiod is the primary factor regulating the activity of the avian testes and that androgen output by the testes is primarily responsible for the displays of the male birds (Wolfson, 1958). Possibly photoperiod, acting via the pituitary and gonads, is the ultimate factor regulating the onset of drumming activity.

Autumnal resurgence of territorial activities in male birds is well documented and is also thought to be under the influence of photoperiod (Marshall, 1952). Thus, it is possible that the autumnal drumming activity in ruffed grouse is also under the influence of androgen output of the testes.

Testicular interstitial cells are known to produce androgens (Marshall, 1952) and a measurement of these cells would presumably give some intication of the relative amounts of androgen produced. The mean sizes of interstitial cells of a sample of ruffed grouse collected in spring, summer, and fall were compared using Duncan's New Multiple Range Test (Steel

and Torrie, 1960). Results are shown in Table 2.

Table 2. Size of interstitial cells of a sample of testes from ruffed grouse collected near the R. B. Miller Biological Station in April, May and July, 1959 to 1960; and September, 1969.

Date	Number of males	Total number of cells measured	Mean size of cells (μ)
April-May	5	50	4.34*
July	5	50	2.62
September	5	50	3.39

* $P<0.05$

These data indicate that the size of cells is maximum in spring, least in summer, and an intermediate size in fall. These results correlate closely with the level of drumming activity occurring in each season. Therefore there is a probable direct relationship between the amount of drumming activity and amount of androgen production of the testes. Note however, that the complete testicular cycle in ruffed grouse is unknown. Also, cells were compared from birds taken in different years and, whereas the fall sample was made up entirely of adults, the ages of males in the spring and summer sample were unknown. These birds were either adults or yearlings.

If drumming activity is primarily regulated by photoperiod, then the onset of drumming activity in spring is accounted for. But each day there are large or small variations in the amount of drumming heard. Possibly other abiotic factors are responsible. However, where observations have been made of displaying grouse, for example in blackcock, it has been shown that abiotic factors have only little effect on the intensity of display (Hjorth, 1966). Although some studies report the influence of climatic factors on the rate of drumming (number of sounds divided by the number of birds producing them) of male ruffed grouse, the studies have had to depend upon the investigators being able to hear the sounds. The drumming performances were not watched. In particular, Sumanik (1966) thought that precipitation and wind were responsible for most of the day to day variation in the drumming rate. Since the drumming count technique has been widely used to estimate population size of male ruffed grouse (Dorney et al., 1958; Petraborg et al., 1953; others), it is important to have a clear indication of the effects of abiotic factors on the rate of drumming. Although my data are few, they are presented since they indicate that, at least during the main part of the drumming season in southwestern Alberta (about 1 May to 15 May), abiotic factors have little effect on the rate of drumming.

Information about the influence of selected climatic factors on the drumming activity of male No. 913 is shown in Table 3.

Table 3. Influence of selected climatic factors on the drumming activity of male ruffed grouse No. 913; May, 1968.

Date	Time	Number of drumming sounds	Weather	
			Wind	Precipitation
5 May	0830-0930	12	light	nil
6 May	0830-0930	14	nil	intermittent light and heavy snow
	1100-1200	16	10 mph	heavy snow and hail
8 May	1100-1200	17	nil	nil

The data indicate that, for the periods of observation shown, wind and precipitation had little effect on drumming activity. Similar results were obtained in 1969. For example, male No. 906 drummed 16 times between 1800 and 1900 hr on 12 May when wind velocity was recorded as "nil". On 13 May, in the same hour, No. 906 drummed 15 times when wind velocity was recorded as "gusting to 15 mph". On both days no precipitation was recorded. No. 906 drummed 11 times between 0445 and 0525 hr on 14 May when there was no precipitation or wind. On 15 May, there was no wind but 4 inches of snow lay on the ground and drumming logs. Yet the male, during the same time interval, drummed 11 times.

These kinds of data indicate that certain climatic factors may not have much influence on drumming males. The results agree with, and add to, those of Gullion (1966), although more work is needed to draw firm conclusions.

5.3 Reproductive Events

The seasonal peak of drumming activity of male ruffed grouse correlates closely with reproductive events. By back-dating from peak of hatch (Fig. 3) the greatest proportion of hens were found to initiate their clutches on 7 May in 1969. Since hens are thought to be inseminated 3 days prior to laying their first egg (Bump et al., 1947), then peak of copulations presumably occurred on 4 May, the same date as peak of drumming. If, as has been suggested, male and female ruffed grouse are promiscuous, and meet only briefly for mating (Brander, 1967; Bump et al., 1947), then some mechanism that "allows" hens to readily accept males when the sexes meet would be advantageous.

The association between the date of the drumming peak and time of mating may be interpreted as follows. If the level of androgen output of the testes initiates drumming in the spring, then the increase in drumming to a peak may be brought about by a stimulating effect of the drum sounds on other males. When drumming activity is first initiated in spring, only very few males are drumming; at peak of drumming, the greatest number of males are drumming (Fig. 5). This is difficult to account for if photoperiod alone was timing

the peak drumming date. Thus, as some males begin to drum their sounds may stimulate other males to drum. As the level of drumming increases hens may be stimulated to seek the males for mating. The presence of hens near territorial males may also influence these males to drum more. In this way, the time of receptivity of hens and drumming activity of the males may be brought to a well-defined peak.

6. ANTAGONISTIC BEHAVIOR

6.1 General

This section deals with a description and interpretation of antagonistic (courtship and aggressive) behavior of territorial male ruffed grouse. Approximately 100 hr of observations were made on 9 different territorial males. Each display or posture was seen from 5 to 10 or more times, except for mating which was not seen.

For the sake of continuity, a general discussion of the reactions of the territorial male to the approaches of other ruffed grouse is made. Then each display is considered separately. All display postures are shown together in Fig. 6 for comparison.

Territorial males leave their logs to approach any other ruffed grouse that are sighted. Before the resident male confronts the trespasser, he appears agitated, moving rapidly back and forth on the drumming log, and occasionally standing fully upright in *alert posture* (Fig. 6c). The resident male may then show *displacement feeding* and/or *displacement preening*.

A displacement activity is defined as an apparently inappropriate activity arising in a conflict situation (Marler and Hamilton, 1966). For example, aggressive behavior is usually made up of attack and escape tendencies---conflicting responses. A bird in such a situation may show irrelevant activity, such as preening or feeding.

Fig. 6. Typical behavioral postures of territorial male ruffed grouse.

a) Resting posture

b) Tail diplay posture

c) Alert posture (Photograph by Mr. R. J. Long)

d) Mating posture (Photograph by Mr. L. C. E. Bogaert)

e) Intensive threat posture

f) Intimidation posture

Note: both postures "e" and "f" were drawn directly from photographs.

a
b
c
d

e

f

Eleven different series of observations of interactions between grouse were made in which the reactions of the resident male were clearly seen before, during, and after, the interaction. In 5, or 46% of the interactions, the territorial male "fed" immediately before approaching an intruder. This activity did not appear to be "normal" since only a few feeding motions were made, and the birds were clearly aware of the intruder as they left their logs, "fed", and returned to their logs several times in rapid succession.

Some displacement feeding appeared to grade into *redirected activity*, which is defined as activity which is appropriate to the situation but is directed towards a neutral object (Marler and Hamilton, 1966). Observations of ruffed grouse showed that, as the resident male approached the intruder, several sharp blows of the bill were directed towards the ground. Unlike feeding, or displacement feeding, the bill was not open and the motions of the bill were very vigorous. This is interpreted as redirected activity since the bill was used in the same manner in fighting (see below).

As with feeding activity, displacement preening was observed. In 8 (73%) of the interactions clearly seen, the resident male preened immediately before approaching the intruder. This appeared to be a displacement activity since it was clear that the resident male had seen the intruder.

Displacement activities in the trespassing grouse were not observed.

Following some displacement activity, the resident male usually drums, then rushes at the adversary in *intimidation display* (threatening posture, Fig. 6f). Now the behavior of the intruder becomes important. If the intruder is a male, he may either flee and be pursued, or he may assume the intimidation display whereupon the resident shows *intensive threat*. In this case attack by the resident is imminent. If the intruder is a female, she too may flee and be pursued, or else she may assume a submissive posture. Then the resident may court her and mating may follow. After pursuit or mating the resident usually returns immediately to the log and drums.

Some observations which were made with stuffed grouse are difficult to interpret. Most notable were those made when the decoy was mounted in alert or resting posture. In all cases the resident male approached the decoy in intimidation display. Soon the male would appear to lose interest and would return to the log and drum. It appeared that some behavioral reaction of the intruder is required before further reactions are elicited from the resident male.

6.2 Resting posture

The position of the body and feathers in resting grouse are considered "neutral" and the posture is described first in order to form a basis for comparison to the antagonistic

displays.

Resting male ruffed grouse may rest fully on their tarsi-metatarsi (Fig. 6a). The wings are held at the sides and the outer margins covered by the lateral feathers of the ventral pterylae. The tail feathers (rectrices) overlap one another and lie naturally in a line with the back. The neck may be either withdrawn, or stretched slightly upwards. Feathers of the capital tract (crest) are raised.

6.3 Alert Posture

In alert posture the bird is standing upright with the body held at about 70° above the horizontal (Fig. 6c). Body feathers are sleeked and the ruffs almost completely hidden. The tail is closed and held in a line with the back. The wings are held as in the resting posture. Only the crest is raised. The alert bird appears prepared for flight or fight. In alert posture the height of the bird is increased and may allow him a better view of his immediate surroundings. As well, the outline of the bird is obscured and he becomes more difficult to detect within the straight lines of the stems and trunks of the surrounding vegetation.

Alarm behavior, an intensive form of alert behavior, may be shown. In alarm behavior the tail is usually partially spread and flicked up and down. The crest is raised, and the ruffs partially lifted. The bird holds himself upright and walks about with short, agitated steps, while uttering a series of liquid "queet, queet---" calls. Flight is imminent.

The partially raised ruffs and spread tail may have an intimidative function, but only until the intruder is clearly recognized. If the intruder is recognized as another grouse, the alarmed bird either drums or shows the intimidation display. If the intruder is recognized as a potential predator, the bird flushes.

These observations suggest that the resident male must be able to see the intruder before the ultimate response is elicited. For example, it was possible to induce a partial intimidation display or alarm posture by rustling the leaves on the forest floor within the blind. Movements of red squirrels (*Tamiasciurus hudsonicus*) would often release the same response. The display was quickly lost but the grouse would remain alert or drum. Similarily, the taped recording of the drumming sound would cause a weak intimidation display, but again visual reinforcement of the stimulus was required before the full intimidation display was elicited.

6.4 Drumming Display

One of the best descriptions of the display is still that of Brewster (*Cited in* Bump et al., 1947:274-275):

> "Suddenly he stretched up his neck...and glanced keenly around...Then he circled four or five times around a space no more than a foot in diameter... and facing at a right angle with the log seated himself on it in the attitude of a

> Penquin...as he sat thus...his tarsi and tail were pressed closely for their entire length on...the log. A moment later the bird began to drum...a quick stroke was given forward; the wings were immediately recovered and another stroke, a trifle quicker than the first, was succeeded by another still quicker,until the wings vibrated too fast to be followed by the eye."

Allen (*Cited in* Bent, 1932) described the manipulation of the tail feathers at the end of the drumming sequence. He noted that the tail of the bird became flattened against the log since he beleived that the forward-upward strokes of the wings tended to drive the bird backwards. He described how at the end of the drumming sequence the bird pitches forwards and the tail springs upwards. He implied that the tail was used to help restore the balance of the bird.

These descriptions are basically correct. However, at the conclusion of the drumming sequence, the bird does not necessarily pitch forwards, nor is the tail necessarily lifted. Thus, after the last thump of the drumming sequence is given, the wings are momentarily held forwards and away from the sides. The primaries are slightly spread open. The wings are then brought slowly to the sides and the primaries closed. As the wings begin to close, the bird raises itself off its tarsi-metatarsi; simultaneously the tail is lifted

from the log, slowly fanned, and the undertail coverts spread. The wings are brought near the sides and held there. At the same time the tail reaches the horizontal, or slightly above it, the rectrices close and drop to lie in a line with the back. As the tail drops the wings are abruptly brought to the sides. In watching the display one is struck by the precision of the movements.

Sometimes the tail is not lifted from the log at the conclusion of the drumming sequence. This shows that raising the tail is not necessarily used as a balance mechanism. Also, the tail is not usually rapidly lifted from the log, but is brought up slowly. These observations suggest that the precise tail movements following the drum are an integral part of the drumming display and are not incidental to it. The manipulations of the tail at the end of the drum are considered to be a *tail display* (Fig. 6b). The similarity between the tail display and intimidation display suggests that the tail display may have an intimidative function.

Previously there was considerable controversy about how the drumming sound is produced. Most commonly, it was believed that the wings struck each other or that they struck the sides of the bird (Bump et al., 1947). Today it is generally accepted that the sounds are produced as the wings are brought sharply upwards and forwards, each striking the air (Hjorth, 1967).

The drumming sound has a slight ventriloquistic quality,

making it difficult to locate the drumming male. Many factors appear to influence the quality of the sound. In particular, I thought that wind, topography, vegetation, and perhaps humidity had some effect. Allen (1934) obtained some evidence that, at least in captive grouse, males drumming for the first time have to practise drumming before the sound can be produced. There is a possibility therefore, that each male may have its own peculiar sound(s), and that birds may learn sounds produced by their neighbors. This suggested that drumming males may recognize individual occupancy of space.

Four to 6 complete drumming sequences were recorded from 7 different males. Amplitude charts of the sounds were made (Fig. 7). Superficially there appears to be no differences among sounds of different birds. Note that each peak on the charts represents one thump of the drumming sequence, and its height the loudness (amplitude).

The time intervals between thumps of each drumming sequence recorded from each male were determined. These interval times were then plotted versus the corresponding thumps. This displays the rhythms of the sounds. Rhythms of sounds of 3 different birds were selected at random and are shown in Fig. 8. All measurements used to determine the rhythms are shown in Appendix 2. The graph for any one male includes all the drumming sequences recorded (4-6) for that male, and each point represents the average value for that interval. There was so little variation between sounds

Fig. 7. Amplitude charts of 6 male ruffed grouse made from taped recordings of the drumming sounds of the males in southwestern Alberta in 1969.

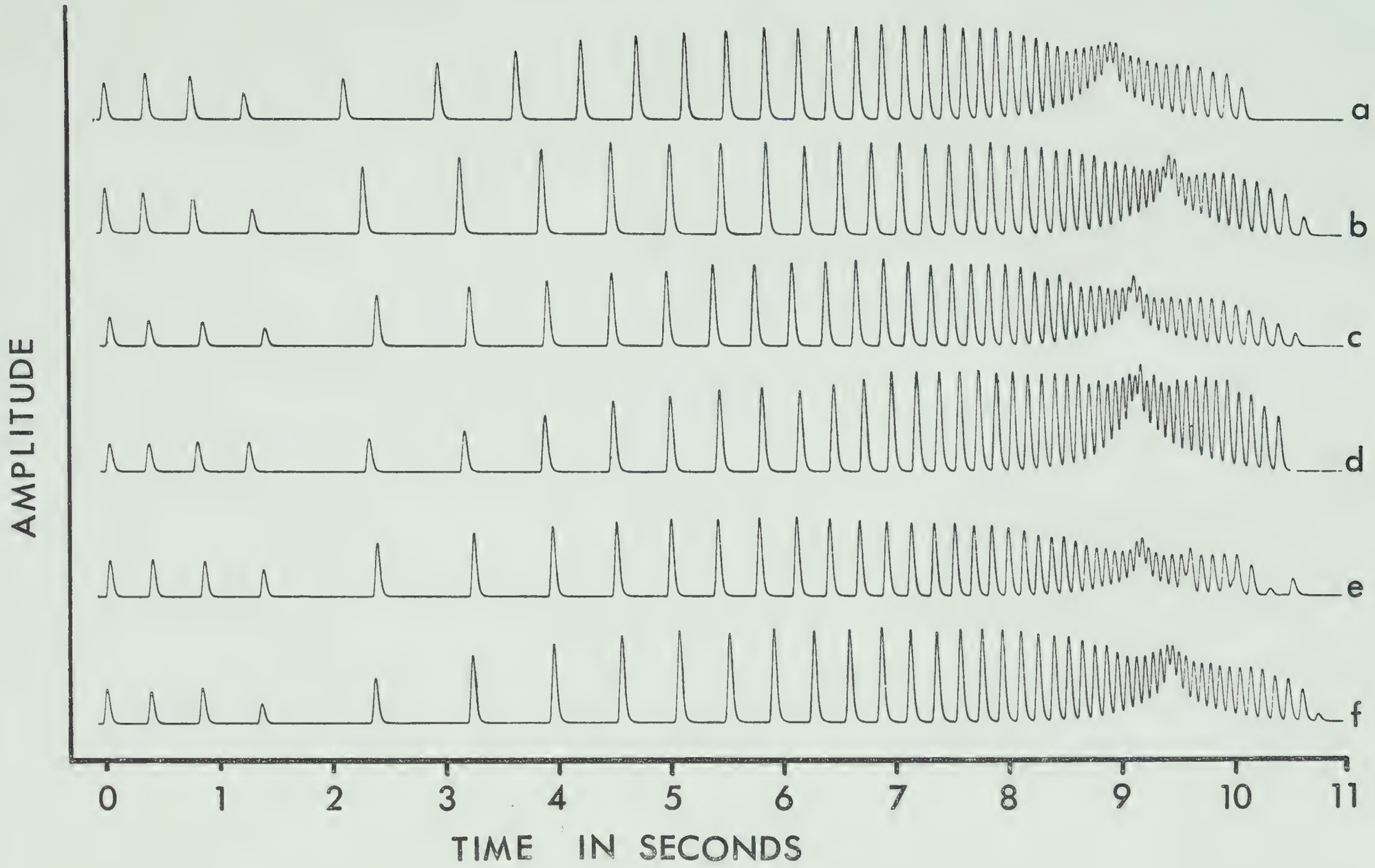
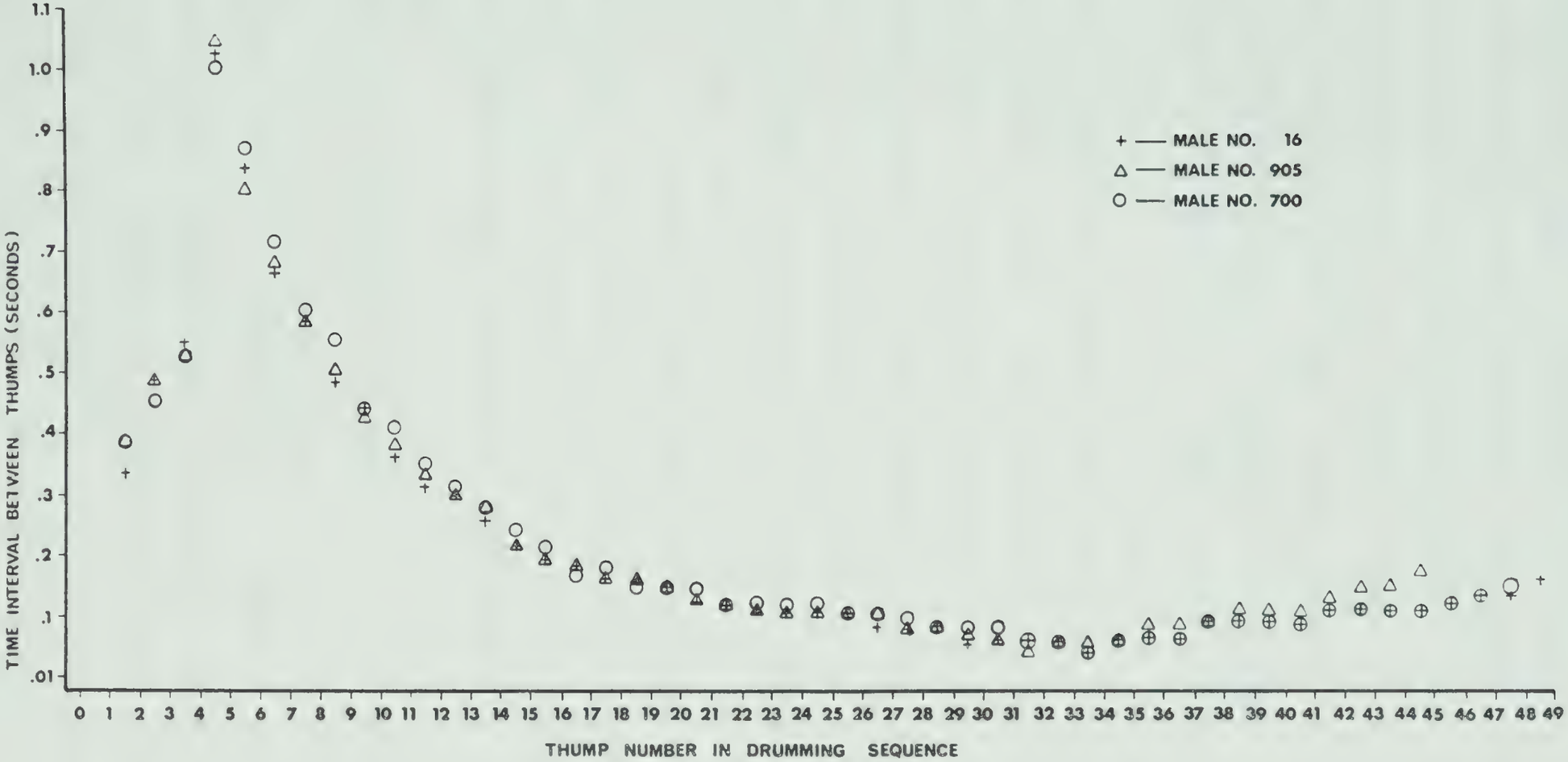

AMPLITUDE
a
b
c
d
e
f
0
1
2
3
4
5
6
7
8
9
10
11
TIME IN SECONDS

Fig. 8. Rhythms of drumming sounds of 3 males, No. 16, 905, and 700, recorded in 1969. Measurements were made from amplitude charts of the sounds.


TIME INTERVAL BETWEEN THUMPS (SECONDS)
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
.01
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49
THUMP NUMBER IN DRUMMING SEQUENCE
+ — MALE NO. 16
△ — MALE NO. 905
○ — MALE NO. 700

for any one bird that most of the interval times were exactly the same for each drumming sequence. The marked similarity between sounds of different birds indicates that there are no basic differences in the rhythms of the sounds.

The most notable difference between sounds was in the number of thumps heard. It should be noted that the number of thumps indicated is two less than the actual number of wing-strokes. My observations showed that two preliminary wing-strokes were made by each bird but they did not register on the recorder. The variations in the number of thumps appeared to depend upon those given at the end of the drumming sequence. It was difficult to tell where they occurred but by counting from the peak of the sound (greatest amplitude) it was found that "extra" thumps occurred only in the last part of the recording. This is not unexpected since observations showed that the drumming male could abruptly end the sequence. The males were never seen to end the sequence near the peak but often after. Sometimes the sequence was ended after the first two or three thumps.

Variations in the number of thumps given may be related to the age of the bird or to the length of time that the bird was established as a drumming male. Although the data are few, these latter suggestions were tested (Table 4). The results show that there is no consistent trend in the number of thumps produced versus the age of the bird or the length of time the bird was established. It appears that the

Table 4. Analysis of the variability in the drumming sounds of a number of male ruffed grouse recorded near the R. B. Miller Biological Station in 1969.

Male No.	No. thumps	Variability index*	Age of bird (yrs)	Length of time the bird was established (yrs)
6	47, 48, 48, 49	2.0	at least 2	1
16	49, 49, 49 49	0.7	at least 2	1
906	45, 46, 46, 47	2.0	at least 2	2
905	44, 44, 45, 45, 45	1.7	2	2
688	47, 47, 47, 47, 47, 47	1.0	3	3
700	47, 47, 47, 48	1.3	3	3

* $\frac{x}{6} x^t$ where x = number of drumming sequences recorded.

6 = maximum number recorded from any bird.

t = number sequences with different number of thumps.

sequences with the fewer number of thumps were recorded from birds that were disturbed near the end of the drumming sequence.

Allen (1934:183) hypothesized that:

> "The drumming of the Grouse...apparently takes the place of the territorial song in other birds. It is an expression by the male of his feeling of superiority. In the spring it becomes an announcement to females, and a challenge to other males."

Some support for this hypothesis was obtained in the present study from observations of drumming male grouse. The following are examples summarized from my field notes.

> 9 May, 1969. Male No. 906 drummed from a single log from 0600 to 0753 hr. He then left the log and was relocated at 0813 hr drumming from a new log (not used in 1969 nor in previous years since no fresh or old droppings were found). After a single drum from the new log, No. 906 assumed the intimidation display and approached a second ruffed grouse about 7 m from the log. The intruder immediately flushed but No. 906 continued to display and made a circuit in front of the log. Only gradually did he sleek his plumage. At 0852 hr he remounted the new log and drummed persistently until at least 0945 hr at which time I left the blind. The new drumming site was used periodically until all drumming ceased in the area on 10 June.

The establishment and use of a new drumming log immediately prior to intimidation display suggests that drumming may be a threat signal.

> 12 May, 1969. A mount of a male ruffed grouse in partial intimidation display was placed on the drumming stage of male No. 905. At 0430 hr No. 905 was sighted moving towards the log in alert posture. When within 1 m of the mount he slowly turned in a tight circle, crossed the log, and circled again. He always kept his head turned towards the mount. Walking slowly,

> and still in alert posture he moved 10 m south and downslope from the site where he mounted a log with no evidence of previous use. There he drummed facing uphill, towards the mount. At the conclusion of the drum the male appeared to lose his balance and to fall off the log. Indeed, this is an unusual drumming position since previous work has shown that males always drum facing downhill when drumming on slopes (Sumanik, 1966). Possibly in the present case this would explain the loss of balance. Nevertheless, after this one attempt at drumming while facing uphill, No. 905 drummed several times facing east, along the length of the log---another unusual position, but one allowing the male to easily keep the model in sight. After each of these drums he turned momentarily to fully face the model in alert posture. Ultimately, drums were made facing downhill but at the conclusion of the drums the tail displays were not seen as the male abruptly assumed the alert posture and threw his head to one side, presumably to look back towards the model. At 0600 hr, No. 905 left the log and could not be resighted.

These observations suggest that drumming is a threat signal, particularily as a new drumming site was established, and as drums were directed towards a "rival". I made similar observations of directed drums (males drumming from unusual positions on old or newly established logs) by male No. 700 on 8 and 13 June, 1969.

In the cases just described there is a possibility that the resident males did not recognize the models as other ruffed grouse. However, the drumming behavior and the alert postures seen are all typical of the reactions of males towards live intruders. Nevertheless, the degree of belligerence did appear to change between days. For example, male No. 905 ignored his mirror image on 10 May, yet the next day

he fully displayed to his image. Reasons for this are unknown, and it was relatively common when working with different birds.

> May, 1968. A grey phase male (color refers to the tail), No. 913, established a territory that year, and used 3 drumming logs. Another bird, a red phase, attempted several times to drum from one of the logs of male No. 913. In each case the red phase was physically driven out by the resident. The red phase bird, subsequently captured and banded, established a territory about 80 m from the nearest log used by No. 913. When the red phase bird began to drum persistently from his territory, No. 913 used a new drumming log east of the logs used previously. The new log lay only 65 m from the log used by the red phase bird.

Again, this case illustrates the circumstances of the establishment of a new drumming log, and indicates that drumming may be a threat signal.

> May, 1969. Male No. 7 used a single drumming log from 28 April to 4 May. No other drumming sounds could be heard from a blind close to this bird. On 3 May, a second bird was heard drumming to the south. This bird could not be located. Male No. 7 was not on his log during that observation period. On 4 May, during morning observations, No. 7 was drumming from his log. Apparently the same bird heard the previous day was heard drumming to the south. For about 1 hr No. 7 remained on his log and drummed persistently. He then left his log and used a new log to the south---closer to the second male. No. 7 drummed persistently on that day for as long as the second male drummed. Subsequently, only the south log was used until at least 6 May, at which time observations were terminated in that area.

Thus, in at least 4 cases the circumstances under which new drumming logs were selected for drumming are known. In all cases there was a direct relationship between interactions with other grouse and the establishment of new drumming logs.

These observations also show that male ruffed grouse have a tendency to face, or direct their drums towards rivals, at least when these latter are in sight of the resident bird. All of these observations strongly suggest that the drumming sound is used to warn other males of occupancy of space.

These series of observations led to the suggestion that if drumming is indeed a threat signal, then the number of drumming logs used could possibly be related to the density of ruffed grouse in any one area.

One test was made as follows. Since 1965, after removal of all the drumming males in the West Area, the population steadily increased to 1968, then declined in 1969 (Table 1). The hypothesis was tested that, as the population of drumming males increased, the number of logs used by each male would also increase. Thus if drumming is a threat signal, one would predict that, as each male came to have more neighbors, they would use more logs to warn these males away.

The average number of logs used per male in the West Area since 1966 is shown in Table 5. These data show that there was no increase in the number of logs used per male as the density of drumming males increased. The results do not show, however, if birds surviving more than one year used more or fewer logs as the population increased or decreased respectively. The table shows both the numbers surviving more than one year and the numbers surviving only one year. Since not all the males on the study area in any one year

Table 5. Comparison between the average number of logs used by drumming males in the West Area to the total number of drumming males, 1966-1969.

Mean number of logs used per male:				Total number of drumming males:			
1966	1967	1968	1969	1966	1967	1968	1969
1.6	1.5	1.6	1.7	17	28	41	36

were banded, the total numbers surviving more than one year is unknown. The banding records show that at least 17 birds have survived more than one year. The number of logs used by this sample of birds was compared to the total number of drumming males on the area each year. The results show that 5 birds surviving more than one year used more or fewer logs as the population increased or decreased respectively. This supports the hypothesis that the number of drumming males does influence the number of drumming logs used. However, 2 birds used more or less logs as the population decreased or increased respectively. This does not support the hypothesis. Also 9 birds used the same number of logs as the population increased or decreased. This does not support the hypothesis. These data indicate that the number of drumming logs used in the West Area by banded males surviving more than one year was not influenced by the total number of drumming birds.

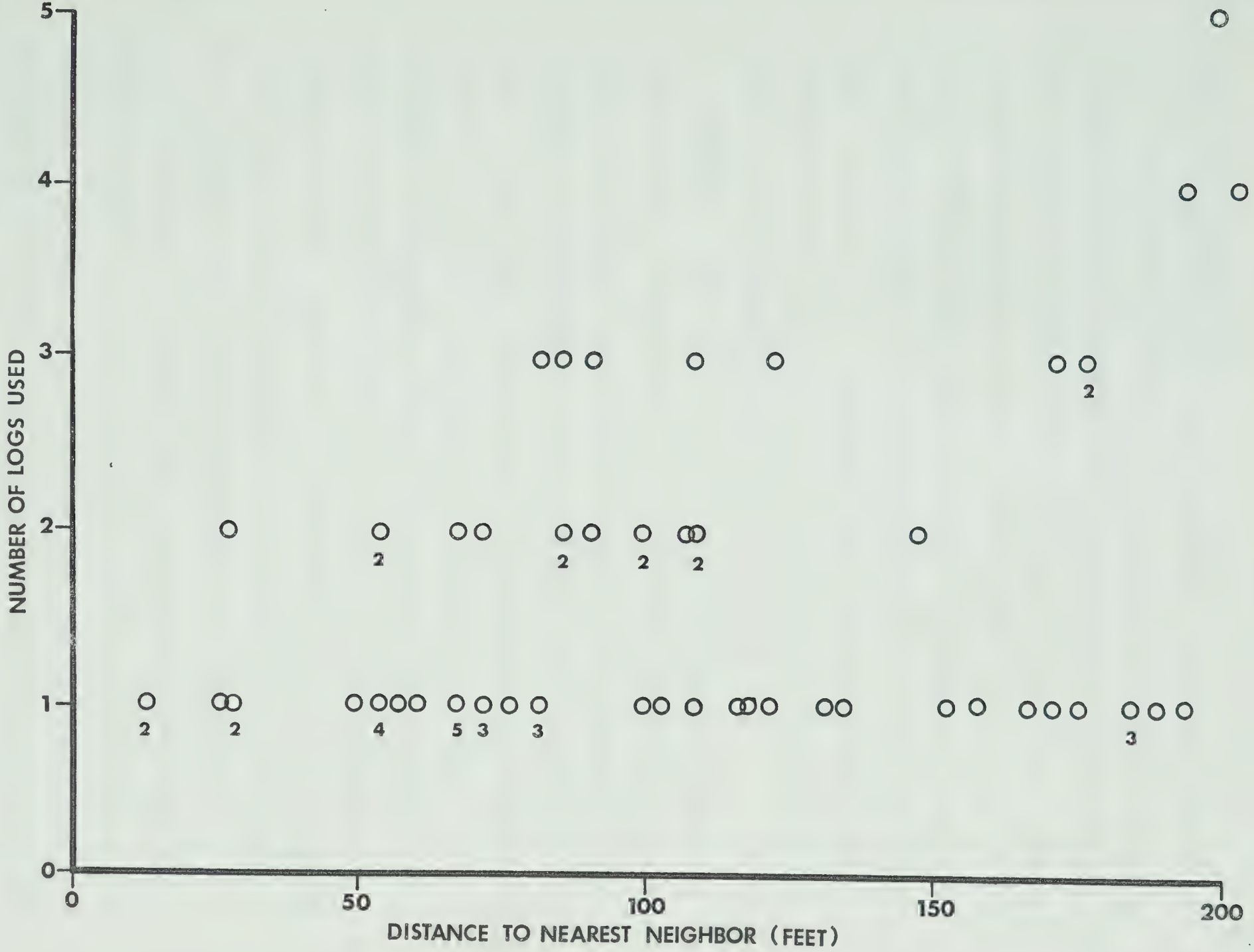
The above test does not show whether birds were any

more dense in a given place as the population increased. Possibly birds used drumming logs scattered throughout the whole area and therefore did not influence the number of drumming logs used by any other bird. Since the distances over which territorial males may influence the activities of their neighbors is not known for certain, a second test was designed to analyze the number of drumming logs used per male in which all the distances between territorial males were considered. Hence, distance was used to give some measure of density.

In the analysis, the number of logs used per male in the West Area in 1968 and 1969 combined was plotted versus the distances to the next nearest neighbor (Fig. 9). If the density of drumming males influences the number of logs used, then one would predict that there would be a direct, inverse relationship between the distances between neighboring males and the number of logs used. However, the results show, if anything, that the number of logs used increased as the distances between males increased. Reasons for this are unknown. The results suggest that, over the distances measured, drumming males do not influence the number of logs used by neighboring birds.

Observations presented previously showed that drumming males sometimes influenced the number of logs used by other males. Considering all the evidence, it is suggested that, only in some cases is the number of logs used by a territorial

Fig. 9. Relationship between the number of drumming logs used (1968 and 1969 combined) by each territorial male in the West Study Area, and the distance to the nearest neighbor in the same study area.


NUMBER OF LOGS USED
5
4
3
2
1
0
0
50
100
150
200
DISTANCE TO NEAREST NEIGHBOR (FEET)

male influenced by the number of other territorial males.

It is possible that at least some of the interactions between birds are between territorial males and non-territorial males. Thus non-territorial males may influence the number of logs used by drumming (territorial) males. Intrusion of hens into territories may also influence the number of logs used. With the available evidence it is not possible to subject these suggestions to analysis. Note, however, that a cohort of non-drumming males has been shown to exist (Dorney and Kabat, 1960; Sumanik, 1966).

Sumanik (1966:30) thought that the number of drumming logs used by a single male "...is probably determined by the number of drumming logs available and by the nature of the vegetation in which these logs are situated." In the present study, there was no indication that the number of drumming logs available was limiting (Table 5). A review of some of the literature (Boag and Sumanik, 1969; Bump et al., 1947; Eng, 1959; Gullion and Marshall, 1968; Palmer, 1963; others) indicates that habitat is important in determining selection for particular logs, but none of these studies give any indication how habitat may influence the number of logs used.

To sum up, it appears that the number of drumming logs used per territorial male may be slightly influenced by other territorial males, and perhaps by non-territorial males. Although habitat may influence the number of logs used, this cannot be shown at present.

The results of the replacement of a drumming male by the taped drumming sound (described in Sec. 4.6) contribute only little to an understanding of the functions of drumming. In the general area where the experiment was conducted, 3 territories were occupied. Two of these were newly established and were occupied by males No. 6 and 18. These territories were 110 m north (No. 6) and 180 m west (No. 18), respectively, from the third territory (the experimental area). Male No. 901 was removed from its log in the experimental area on 2 May and the first artificial drumming sound played from its log on 3 May.

Male No. 6 was captured in one of the trap cells in the experimental area within 24 hr after No. 906 was removed--- and before the first artificial sounds were played. No. 6 was released near the trap cell and was subsequently observed from a blind where he drummed from his own territory. On 17 May he was captured in the experimental area again. Only from 3 to 9 May was the artificial sound played. Thus No. 6 was captured 8 days following the last sequence of artificial drums. Thus male No. 6 only moved into the experimental area when no drumming sounds were played, suggesting that the sound was sufficient to announce the presence of a resident "bird".

In September, male No. 6 was shot on a drumming log 40 m east of the log used by male No. 18. Male No. 18 was seen the same day on the log in the previous experimental area.

These observations may be interpreted as follows. Males

No. 6 and 18 were newly established birds. It is known that in the establishment of a territory, newly recruited males will explore a number of drumming logs before final selection is made (Brander, 1965; Eng, 1959; Gullion, 1967). It appears that in spring male No. 6 explored an alternate territory (that of male No. 901), but only when it was not occupied. In fall, both males No. 6 and 18 explored other sites. Both sites were unoccupied at that time. Possibly male No. 6 forced No. 18 from its territory so that No. 18 moved into the previous territory of male No. 901. However, if No. 18 was forced from its territory, it would seem that No. 6 would have used the vacated log which he did not appear to do. Also note that male No. 6 had already used the log in the experimental area at least twice in spring. It seems likely that he would have returned there if it wasn't already occupied. Thus, male No. 18 may have moved to the experimental area before male No. 6 moved into the territory of male No. 18.

The effects of the natural or artificially reproduced drumming sound on the activity and behavior of male ruffed grouse give some additional evidence that drumming may indeed be a threat signal.

The taped drumming sound or phonograph record of it played back in occupied territories usually elicited a partial intimidation display from the resident males. Two examples of the effects of the sounds are summarized below.

> 10 May, 1969. Male No. 700 was drumming from a log about 30 m from the blind where the sound was played. After a series of playbacks of the

> sound, the male ran to a log about 10 m from the blind and drummed. While moving to the log he directed several sharp blows with his bill to the ground. For every playback of the sound, the male either drummed or turned to fully face the blind in alert posture.

Since the sound was played in the territory of this male, the results are most easily interpreted as follows. The "intruder", the playback of the drumming sound, drummed within the territory of male No. 700. The resident responded by approaching the "intruder" and threatening both by drumming and redirected pecking activity. Unable to locate the intruder, No. 700 drummed periodically from a nearby log.

> 18 May, 1969. Male No. 6 was drumming from a log about 8 m from the blind. The recorded drumming sound was played from the blind at irregular intervals throughout the observation period. A heavy rain was falling, which then turned to hail. During the period the male left the log 5 times to roost under a spruce tree near the log. Each time he remained there for about 1 to 2 min before returning to the log to drum. Near the end of the observation period the male was wet and bedraggled. This was the only case recorded where a male allowed himself to get so wet.

It would appear that the sound stimulated the male to repeatedly return to its log to drum.

These two series of observations suggest that the drumming sound has some influence on the behavior of drumming males. However, in some cases it was difficult to tell if the sound was having any effect at all. If a male was on, or near his log, then the sound would provoke a partial intimidation display and the male would investigate the sound. If the male was not near, or on, his log, then the sound

would not "call" the bird into sight. It seemed that the male had to be active before the sound would elicite any response.

Since the sound did have some effect on the behavior of males in some cases, the effect of the sound on the rate of drumming was investigated.

In the first test, the rate of drumming of one bird was compared to the rate when 2 or more birds were drumming. Data obtained from the transect runs were used. At each listening stop the number of sounds heard in 4 min was divided by the number of birds making the sounds. Data collected from 27 April to 9 May, 1969, were used. The data represent the number of sounds heard at 13 listening stops. Each stop was visited 7 times; some stops (7) were visited an additional 3 times.

The results of the calculation of the rate of drumming at all stops is shown in Table 6. The increase of 32% in the drumming rate when 2 or more birds are drumming is significantly greater than the rate when one bird is drumming ($P<0.05$; Mann-Whitney U-test (Siegel, 1956)).

In another test, the effects of the playback of the recorded sound on the rate of drumming was determined. On 1 June, 1969, the sound was played at 2.5 min intervals every second half hour (0450-1600 hr) from a blind in the territory of male No. 16. The mean rate of drumming (4.60) when the sound was played (11 half hour intervals) was 34% higher ($P>0.05$) than the mean rate (3.44) when the sound was not played (12 half hour intervals). Means were compared using

Table 6. Comparison of the rates of drumming (number of sounds heard divided by the number of birds making them) when one bird is drumming compared to the rate when two or more are drumming. Data represent the mean number of sounds heard daily at 13, 4-minute listening stops along the Forestry Reserve Road from mile 4.5 to mile 12.5, from 27 April to 9 May, 1969.

Number of birds drumming per listening stop	Number of stops	Mean drumming rate
1	19	1.11 *
2 or more	84	1.46

* $P<0.05$

the Mann-Whitney U-test (Siegel, 1956).

Since a 32% increase in the rate of drumming was significant using the road-side drumming count technique, and the 34% increase was not significant using the playback of the drumming sound; and since the same statistical test was used, it is likely that the sample size used to calculate the 34% increase was inadequate to detect the difference.

The increase in the drumming rates may be interpreted as follows. A male ruffed grouse when threatened by drumming will return the threat by drumming. If this is so then one

might expect male A, for example, to drum the same number of times after male B, as male B drums after male A.

To test this suggestion, data from 2 different areas were examined. Males were compared 2 at a time, and the time interval between their drums was ignored. The results of the test are shown in Table 7. These data indicate that each male drums the same number of times after every other male (chi-square tests; $P \geq 0.05$). This suggests that the birds are answering the drumming sounds of their neighbors. If this is so, and if drumming is a threat signal, then each male fully defends its territory. However, each male does not drum at the same frequency as every other male. Reasons for this are unknown. It may simply be a reflection of the vigour of the birds, or perhaps the lengths of time that the birds held territories. In either case it would suggest that threatening, and hence defence of space, is stronger in some birds than in others. Possibly birds that drum with a low frequency are newly established birds that have developed some attachment to a site but are also exploring other areas.

Does the drumming sound attract hens to the drumming logs of the males? Female ruffed grouse are much more mobile than the males in spring (Hale and Dorney, 1963). This would suggest that the hens come to the males for mating. Several studies have reported that hens visit the males at their drumming logs (Brander, 1967; Evans, 1961; Grange, 1948; Wing, 1938). Whether the sound attracts them, however, is unknown. If ruffed grouse are promiscuous, as has been suggested,

Table 7. Comparison between the number of times any male ruffed grouse drums after every other male. Sounds heard near mile 4.5, Forestry Reserve Road, 27 April, 1969, from 1725 to 1925 hours.

A/B	B/A	A/C	C/A	A/D	D/A	A/E	E/A	A/F	F/A
4	7	15	11	2	3	1	2	5	6
B/C	C/B	B/D	D/B	B/E	E/B	B/F	F/B	C/D	D/C
2	4	1	3	1	0	1	1	2	0
C/E	E/C	C/F	F/C	D/E	E/D	D/F	F/D	E/F	F/E
1	0	5	5	0	0	0	0	1	0

5 May, 1969, 0530 to 0830 hours.

A/B	B/A	A/C	C/A	A/D	D/A	A/E	E/A	A/F	F/A
8	8	12	13	0	1	4	1	1	2
B/C	C/B	B/D	D/B	B/E	E/B	B/F	F/B	C/D	D/C
11	9	2	2	1	5	3	1	1	1
C/E	E/C	C/F	F/C	D/E	E/D	D/F	F/D	E/F	F/E
3	1	3	3	1	2	0	0	1	0

Mile 5.0 Forestry Reserve Road, 12 May, 1969, 0400 to 0433 hours

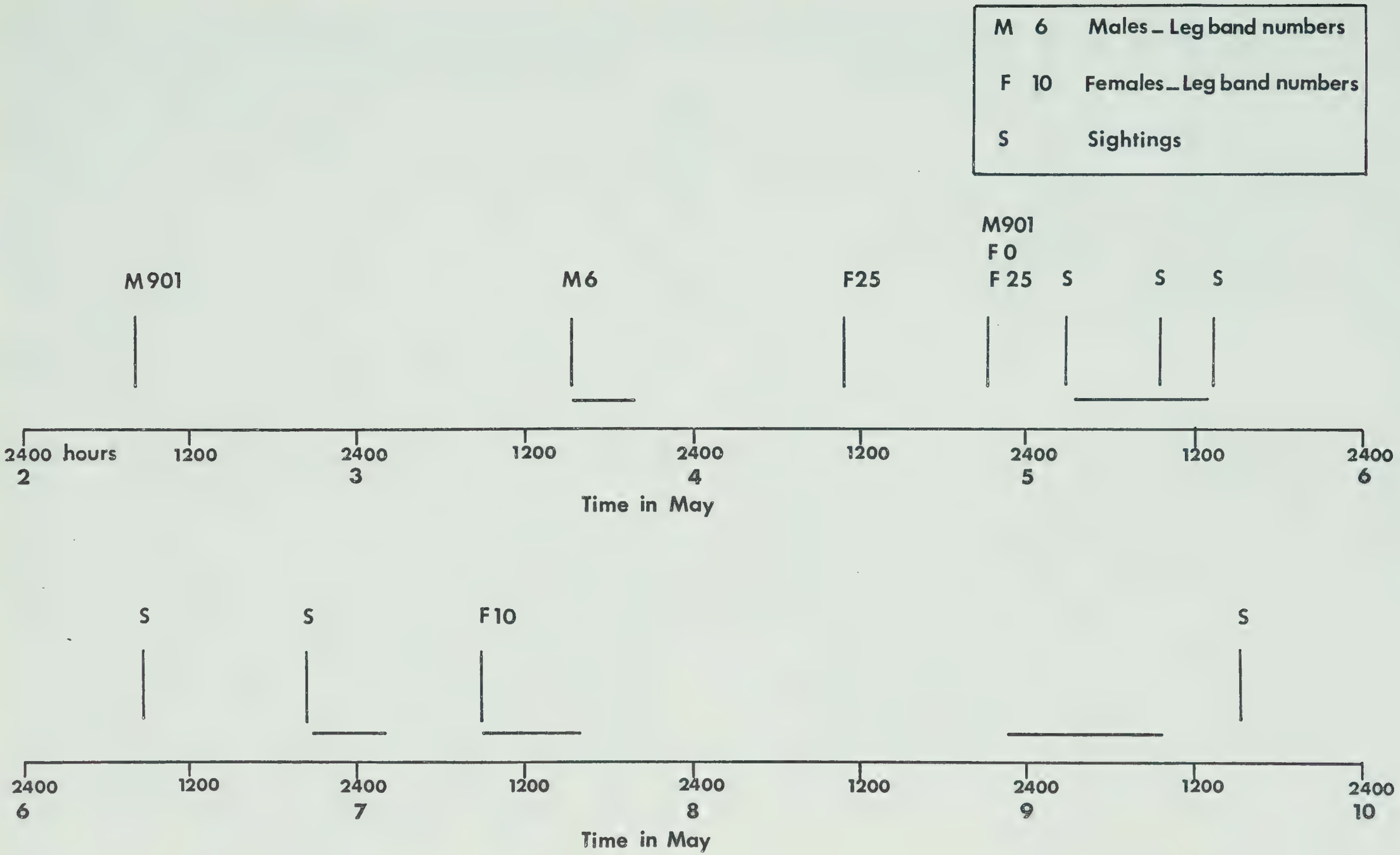
A/B	B/A	A/C	C/A	A/D	D/A	A/E	E/A	B/C	C/B
3	2	5	4	1	4	1	0	1	2
B/D	D/B	B/E	E/B	C/D	D/C	C/E	E/C	D/E	E/D
3	0	0	0	3	4	1	1	0	1

(Brander, 1967; Bump et al., 1947),then some mechanism that would aid the hens in finding the males would have survival value for the species.

The results of the replacement of a drumming male with the taped drumming sound are summarized in Fig. 10. Two males (No. 6 and 18) captured during the experiment have been discussed previously. The third male, No. 901, was removed from the experimental area and released 1 mi west of its territory. He was recaptured in his territory on 4 May, and was in a trap cell with a hen. Since the hen was badly hurt attempting to get out, and the male was not, it seems that the hen was caught first, and the male followed her in later. It is unlikely that the presence of the male influenced the capture of this hen. No. 901 was then moved 1.5 mi east of its territory and was not seen again.

Three hens were captured during the experiment, or 1 hen per 2.3 days. Broadly, these results show that hens come into seemingly occupied territories. However, the experiment was improperly controlled so that it is not possible to determine whether the sound attracted them. It was thought that by playing the sound for a given interval of time every second day the same trap scheme could be used as its own control. Then a comparison could be made between the days when the recorder was on to when it was off. However, no hens were caught during the interval when drumming was played, but only after. The time

Fig. 10. Results of an experiment designed to test the functions of drumming. Horizontal bars represent periods when the taped drumming sound was played. Vertical bars show some of the times when traps were checked. Bird "sightings" refer to unbanded ruffed grouse that were seen near the trap cells but which were not caught. Male No. 901 was the resident bird in the area.


M 6 Males – Leg band numbers
F 10 Females – Leg band numbers
S Sightings
M901
M6
F25
M901
F 0
F 25
S
S
S
2400 hours
1200
2400
1200
2400
1200
2400
1200
2400
2
3
4
5
6
Time in May
S
S
F10
S
2400
1200
2400
1200
2400
1200
2400
1200
2400
6
7
8
9
10
Time in May

intervals between captures and drumming sounds are maximal as they are the times at which the traps were checked. Usually the traps were checked three times daily, at approximately 4 hr intervals. Therefore the hens may have been caught much closer to the time that the drumming sounds were played. Yet it is clear that no hens were caught during the interval when drumming was played. Thus the question as to whether the sound attracts hens remains unanswered. Reasoning from the differential mobility between the sexes and the promiscuous breeding habits of the species, it would seem plausible that the sounds are attracting hens.

6.5 Intimidation Display

When other ruffed grouse are seen, or grouse-like sounds are heard, the territorial male assumes the intimidation display (Fig. 6f). Intimidation posture is assumed slowly with precise patterns of feather manipulations. Male ruffed grouse in intimidation display appear to increase at least twice in size. The dark, iridescent, black or red-brown ruffs are slowly erected. The tail is slightly lifted and the rectrices spread; the long, white-tipped under-tail coverts are exposed. The wings are lifted slightly from the sides, drooped, and the primaries opened. The legs are extended, and the back of the bird held horizontal to the ground. The neck is held perpendicular to the body. The tail and ruffs are elevated until the latter form a full circle about the head, and the tail is fully fanned and held

perpendicular. At an undetermined point in the sequence, the auriculars are spread out from the sides of the head and the crest is lowered.

In full intimidation display the male then displays various feather groups towards the intruder. Except in intensive threat the male never fully faces the intruder --- a quartering view either towards or away from the intruder is presented. However, the whole tail fan and neck and head may be tilted towards the rival. Various head and neck movements are now seen. First the head is shaken from side-to-side with a pause between each shake. At the same time the ruffs are rapidly rotated around the sides of the neck. The head and neck may then be *scooped*. The neck is thrust outwards and swung downwards and to the side. The head is snapped to the same side. The neck is then rapidly withdrawn, being swung upwards and to the opposite side. Simultaneous to these movements the ruffs are rapidly rotated. Several sharp blows of the bill may be made to the ground at this point. These movements accentuate the ruffs, which appear as an iridescent blur against the drab tail fan and may also display more fully the little-developed yellow or orange eye combs.

The male has been stationary but now he rushes at the intruder in an arcing path with a series of short rushes interspersed with stops of short duration. At each stop head movements are performed. With these movements

the male may hiss and/or utter a low volume, low frequency, coughing sound. If the trespasser flushes or runs away immediately, the displaying male stands still and fully upright. The legs are extended and the back held parallel to the ground. The neck is stretched upright. The male may then move very slowly to the spot where the intruder flushed with his head bobbing back and forth and the whole tail fan tilting slowly from one side to the other. After these slow, apparently exploratory movements, the cock may lower his tail and partially collapse his ruffs. The wings are closed and folded normally at the sides. The male, when returning to the drumming log, walks upright on stiff, straightened legs, with the neck stretched upright and the head bobbing back and forth. The tail is held horizontal to the ground and may be flicked up and down. The male usually mounts the log and immediately drums.

If, when approaching the intruder, the intruder remains stationary and does not display (intimidation) the territorial male may move, in full intimidation display about the trespasser, stopping periodically to drum. No drumming stage is selected; rather, the cock may drum from the ground, or any convenient elevated object. Observations made with stuffed grouse showed that, after some display of variable duration, the territorial male ignored the model. In most cases a live intruder flees at first rush of the displaying male. The intruder may, however, assume the intimidation display. In this case the territorial male usually drums, then immed-

iately shows intensive threat. Attack is imminent.

The territorial male never directly approaches the trespasser. The whole display appears to accentuate certain feather groups, notably the ruffs and tail. These and the rush seem to intimidate the trespasser so that in most cases the trespasser immediately flees. In studies of captive ruffed grouse it has been shown that a displaying male will eventually attack an intruder (another grouse placed in the same pen). Even if the intruder is a male and assumes a submissive posture, it may be either violently attacked or mounted in attempted copulation (Allen, 1934). This was not seen in the field and may be explained as follows. In a territorial system, withdrawalof the intruder is just as important in determining the outcome of an interaction as is the attack by the resident (Tinbergen, 1957).

The purposes of the vocalizations in intimidation display are unknown. Possibly they may arise from excitement and convey no information to the rival. Attempts to record these sounds so that they could be played back failed.

In summary, I agree with Hjorth (1967:241) that the major function of the intimidation display is to force the opponent to "confess sex and status".

6.6 Intensive Threat

In intensive threat the male holds the body low to the ground with the legs flexed (Fig. 6e). The wings are closed

and held at the sides, but may be held higher than in the resting position. The neck is fully extended and held in a line with, or slightly lower than, the back. The tail is folded but is held below the horizontal. The crest is elevated, and the ruffs are inconspicuous. In contrast to intimidation display, all feathers are depressed and no group of feathers is conspicuous.

In intensive threat, the male runs continually, in a zig-zag pattern, back and forth in front of the intruder. The cock may turn in small, tight, circles on the log or ground, and direct sharp blows with the bill to the substrate. Soon a rush is made at the adversary. In all cases recorded the intruder immediately fled, either by running or flying away. The resident male always pursued.

When the display was elicited by mirrors, the threatening male physically attacked his image. Blows appeared to be given mainly with the bill and seemed to be directed at the head of the "rival". Sometimes following a zig-zag rush at the image, the cock would spring into the air with the legs extended forward and the wings buffeting the air and "rival". After recording one or two sequences of direct attack, the mirrors were retrieved in order to prevent injury to the male.

Sometimes the male would stand upright and motionless in front of the adversary (mirror). This posture was very similar to alert posture. The function(s) of this posture in

intensive threat is uncertain, but may indicate direct frontal attack. In spruce grouse (*Canachites canadensis franklinii*) a similar posture is seen under the same circumstances (MacDonald, 1968).

6.7 Courtship

The courtship behavior of male ruffed grouse has been divided into three phases (Allen, 1934):

1. *Strutting phase*: The territorial male assumes the intimidation display and confronts the intruding grouse; both males and females are driven off.

2. *Gentle phase*: The male loses interest in territory; he follows the female about; instead of erection of feathers, they are depressed. When another grouse is seen, he attempts copulation.

3. *Fighting phase*: The male may strut; usually he assumes the intensive threat posture when confronting other grouse.

These descriptions were based on observations of penned birds. Although field observations are few, they do not indicate that the behavioral patterns are similar to those seen in captive grouse. Allen (*Cited in* Bump et al., 1947:282) described different patterns when observations were made with a wild male. When a female in a wire crate was placed near the drumming log of the male, the latter strutted for about three quarters of an hour, then immediately attempted to mate with the hen through the wires of the crate. Following this, the male ignored the hen and began drumming.

Evans (1961) described the interaction between a territorial male and what was thought to be a female. The male went through what appeared to be a normal intimidation display. However, the hen ignored him and flew away. The male returned to his log and drummed.

Allen (1934) believed that the "gentle phase" may last for up to one week---during this time territorial activities are ignored. However, during the observations made in the present study nothing resembling a "gentle phase" was seen. In all cases the intruding grouse were confronted in intimidation display. In at least 2 cases I thought that the intruding grouse may have been females. Instead of fleeing, and unlike intruding males which, if they attempt to stay in the vicinity will assume the intimidation display, both these grouse first avoided the male by flying into trees. The resident male continued to display then flew into the tree to roost beside the other grouse. Before it was possible to observe the outcome of these interactions, it became dark and the observations were ended. If these intruders were females it is possible that the resident may have assumed a "gentle phase" subsequently. However, territorial males were never seen to relax their belligerence towards trespassers and assume a "gentle phase". Yet the absence of obsering this behavior does not mean that it does not exist.

Perhaps the best descriptions of courtship were made by Mr. Keizer and Mr. Bogaert (*pers. comm.*). In their

observations a territorial male went through what appeared to be a normal intimidation display towards a stuffed hen. The hen was stuffed in a squatting position with all the feathers sleeked. The hen was approached by the male in an arc in short rushes, with "head shaking", "scooping" and "pecking". No vocalizations other than "hissing" and "coughing" were heard. The male moved behind the hen at the end of one rush and, without additional display, mounted it by placing one foot then the other on its back. Leaning forward, he grasped the crown feathers of the mount, lowered his wings to either side and attempted, by lowering his tail, to make cloacal contact. From the wetness on the rump of the mount, it seemed that the male had ejaculated semen. The male remounted the hen several times and, both while on and off the hen, remained in at least partial intimidation display. Observations with the same male were made over several days and activity each day was similar.

These observations indicate that the "gentle phase" may be a result of effects of captivity on birds. Also, the observations indicate that courtship and threatening in male ruffed grouse are not very different.

6.8 Summary

The antagonistic displays of male ruffed grouse are based on the erection and presentation of various feather groups, notably the ruffs and tail. These feathers are accentuated by their movements in display. Erection of the

feathers without associated movements provide cryptic patterns against the forest background.

The differences between courtship and aggressive behavior are only readily apparent in the consummatory act (mating or attack, respectively).

Two major displays in antagonistic behavior are drumming and intimidation displays. Drumming appears to: (1) attract mates, and (2) warn other males of occupancy of space. Intimidation display apparently elicits the appropriate behavior from intruders: fleeing in males and mating posture in receptive females.

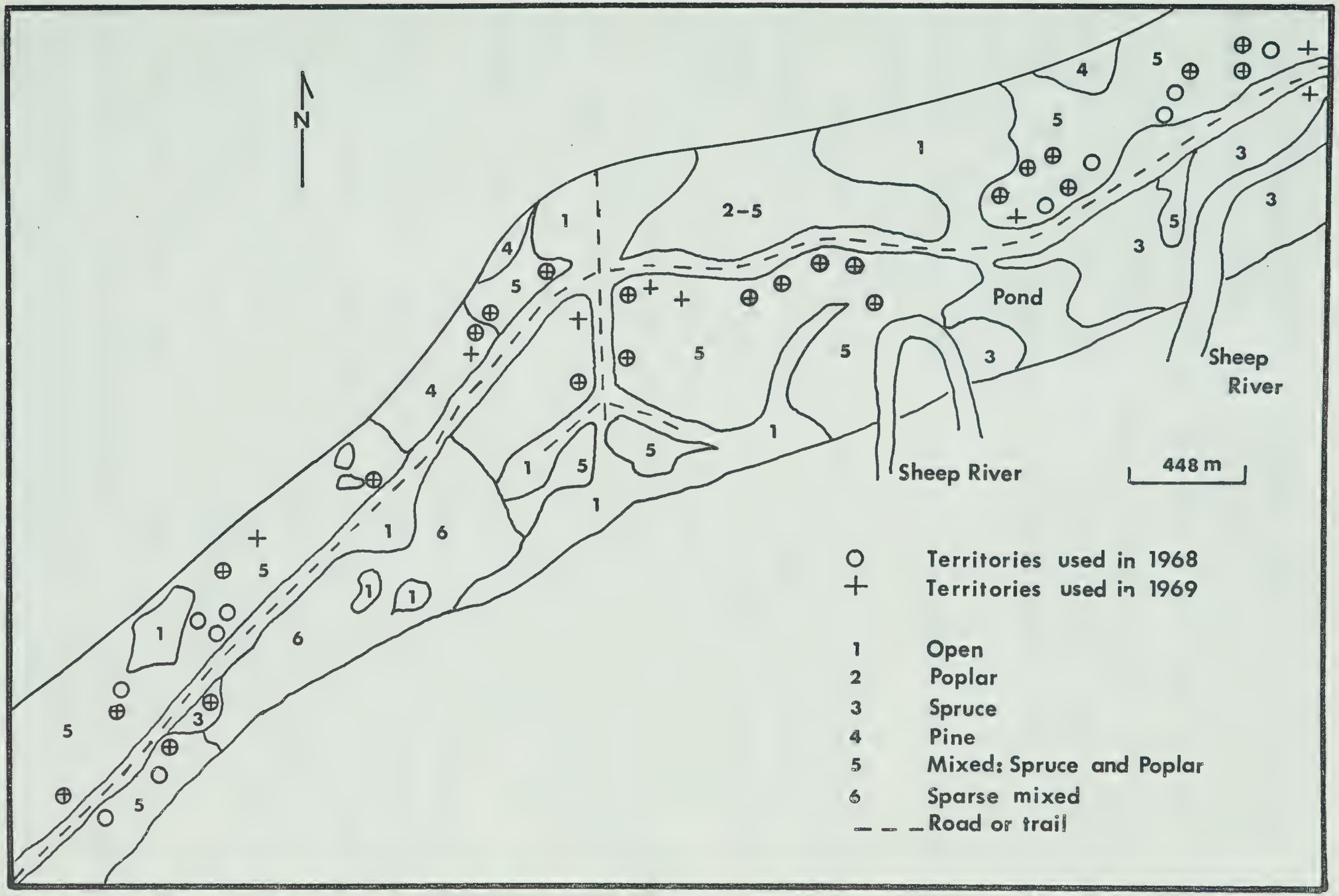
7. TERRITORY

7.1 Dispersion of Territorial Males

Dispersion of territorial males is considered only in the West Area, where forest cover is nearly continuous, and the number of males is considered to represent an adequate sample size. The two main factors governing dispersion are probably habitat and social interaction. Both are considered.

The distribution of territorial males in 1968 and 1969, when the highest numbers of males were censused, is shown in relation to several different plant associations (Fig. 11). Different plant associations were determined from aerial photographs of the area. Clearly, most territories were established in mixed wood of spruce and poplar. But since mixed wood makes up the greatest proportion of habitat on the area, it is difficult to determine if such habitat is being selected for. That some selection is being made by male ruffed grouse has been indicated by Boag and Sumanik (1969). They compared vegetation around used drumming logs to logs not used for drumming. Two major differences were found: at used sites, (1) the density of stems, but not of canopy cover, of young trees (shrub-size) was greater; and (2) the canopy coverage and frequency of young white spruce was greater. It was concluded that selection for such characteristics was possibly made on a basis that allowed the drumming males to see the approach

Fig. 11. The distribution of territories in relation to several broad catagories of vegetative types, on the West Study Area in 1968 and 1969.


N
Pond
Sheep River
Sheep River
448 m
Territories used in 1968
Territories used in 1969
1 Open
2 Poplar
3 Spruce
4 Pine
5 Mixed: Spruce and Poplar
6 Sparse mixed
Road or trail

of other grouse or ground predators, and at the same time effectively screen the birds from avian predators.

Eng and Gullion (1962) determined that most losses in a population of ruffed grouse in spring were due to avian predators, and that territorial males were the most vunerable. Later, Gullion and Marshall (1968) determined that a smaller proportion of drumming males were taken on their logs than elsewhere, and that some of the sites selected significantly increased longevity.

Therefore selection of areas for establishment of territories by male ruffed grouse is probably influenced by habitat. Selection seems related to characteristics that afford protection from potential predation.

Particularly in spring, there appears to be an abundent food supply for ruffed grouse, so that selection of areas for the establishment of territories does not seem to be related to this factor (Bump et al., 1947).

Eng (1959), Gullion (1967) and Palmer (1963) suggest that social interaction may also influence the establishment of territories. According to this suggestion, newly recruited male ruffed grouse establish territories near those of older, territorial males. Only little evidence was presented to indicate that this is so. In fact, Gullion (1967) hypothesized on the basis of the observed distribution of drumming males that ruffed grouse are an incipient lek species, where clusters of males, distributed over an area termed a "lek", perform a group (communal) drumming display. Note that

some clumping of drumming sites is evident in the West Area (Fig. 11), which may indicate that birds already established on territories are influencing other males to settle near them, thus establishing a "lek".

In the present study two tests were made to consider the extent that social interaction may govern the selection of drumming sites. In the first, each drumming site in the West Area was paired with its nearest neighbor and the two were scored for each of four years (1966 through 1969) as "both occupied", or "one of the two occupied". As a comparison, each site was paired with another in the West Area selected at random. Occupancy of these pairs was scored as for neighboring pairs. If there was a tendency for established males to influence the occupancy of adjacent sites one would expect a different pattern of occupancy of adjacent sites as compared with sites selected at random. The results show that neighboring sites were occupied in the same year 67 times, and one of the two was occupied 74 times. In the pairs matched at random, both were occupied 68 times and only one of the two, 78 times. These results indicate that the occupancy of adjacent sites were independent. Therefore in this test, clumping of drumming sites cannot be explained by the influence of territorial males on newly recruiting birds. Presumably, clumping results from attractiveness of habitat.

Another test of association, a one-sample runs test (Siegel, 1956) was used to distinguish between random and successive yearly use of drumming sites. There was no sig-

nificant departure from random use ($P>0.05$). This suggests that the occupancy of a specific drumming site in a specific year had no influence on whether it will be occupied the succeeding year.

The results of these two tests further support the suggestion that drumming sites are selected mainly on the basis of habitat.

The clumping of sites might indicate that male ruffed grouse are not territorial, or else defend a very small area. Yet the observations discussed previously showed that aggression could lead to spacing out of drumming males (Sec. 6.4). To examine this more closely, the distances between a sample of territories were measured. Measurements were made from the drumming log, or from the geographical center of a number of drumming logs to a similar point in the neighboring territory. For these measurements, the greatest local density of sites - those north of the pond, plus some just west of there (Fig. 11) - were used. In all, thirteen measurements were made. These values were then divided by two, and the resulting distances averaged and used as a radius of a circle surrounding each male. The mean area of the circle was found to be 1.4 acres which may represent an average space requirement of each male. This area is remarkably similar to the 1 to 2+ acres recorded to be used by male ruffed grouse in other populations in spring (Eng, 1959: Fowle, 1953).

To sum up, it is concluded that territorial male ruffed

grouse establish territories mainly on the basis of habitat. Further, there is no evidence that newly recruited males are influenced to settle adjacent to males already holding territories, or that territorial males successively reuse territories as they become vacant. It does appear that the presence of a territorial male does prohibit another male from establishing within a set distance.

7.2 Use of Territories

To examine the use of territories data gathered from observations were summarized for each observation period for each male. These data were grouped into daily and seasonal periods. Three daily periods were defined: morning display period (0330 -0930 hr); mid-day interval (0930-1630 hr); and, evening display period (1630-2000 hr). Two seasonal periods were defined: early season (27 April-15 May) and late season (16 May-1 June).

From the data, the average proportion of each observation period a male spent in each separate activity was determined. These data were related to the daily and seasonal periods defined above, and to the influence of weather (mostly analyzed previously).

Many repeat observations of three males, No. 7, 906 and 913, were made. Observational data of each were treated separately. Six other males were observed for lesser lengths of time. Data from these were combined, and a single *hypothetical male* was derived. This was done because it was thought that too few observations were made on each male to warrant a separate analysis.

For each of the birds considered a field map of their activities was prepared (Sec. 4.3). The map of the hypothetical male was derived as follows. The number of drumming logs used by each of the six males was determined. In some cases only one was used, in others two. Examination of the field maps showed that the alternate log always lay in a westerly direction to the primary log. This was fortuitous since it was then possible to determine the average distance between the logs and plot the alternate log on the map of the hypothetical male as lying due west of the primary log and the average distance from it. The field maps of each of the six males were then divided into four quadrats (NE, NW, SE, and SW) by drawing perpendicular lines through, and extending outwards, from the primary log.

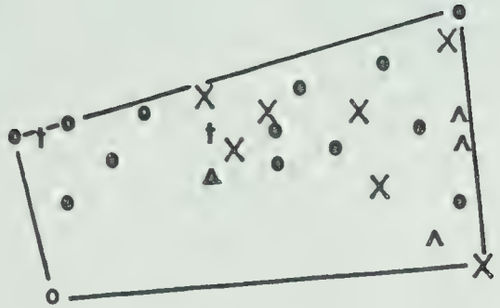
The distances from the primary log to points of observation of each male for each activity in each quadrat were averaged. For example, if a male fed in the NW quadrat 30 and 60 ft from the primary log on two separate occasions then an average distance (30+60/2=45) was determined for that activity in that quadrat. This point was then replotted as lying exactly mid-way between the arms of the quadrat. When these calculations were all made, the map of each of the six males were then represented by a series of points in each quadrat. Each point showed the average distance moved for each activity in that direction. The outermost points of sightings in each quadrat were plotted separately. When all the field maps of each of these six males were treated

as discussed, the points in each quadrat for each activity were averaged for the six males. For example, if each of the six males interacted in the SE quadrat at 6, 9, 4, 30, 2, and 15 ft from the primary log, a single point was plotted in the SE quadrat of the map of the hypothetical male 11 ft from the primary log.

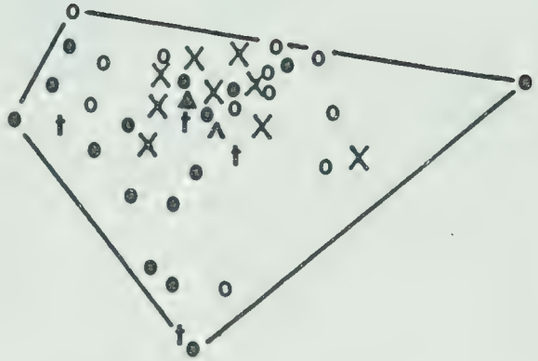
The field maps of the four males (hypothetical, No. 7, 906, and 913) are shown in Fig. 12. In Table 8 is shown the analysis of the activity of each of the males. All the data on which the calculations of the hypothetical male are based are shown in Appendix 3. Included are the field maps of each of the 6 males.

The time the whereabouts of each male was known was highest for the early season, morning display period. This reflects the large proportion of time the birds spent in the immediate vicinity of the logs. The early season period corresponds to the peak reproductive period. During this time most of the drumming activity was performed and most matings took place. The large proportion of time spent near the logs at this time further suggests that hens must seek out the males to mate. Note that the value for the same period for the hypothetical male is much less than that for the other males. This may simply reflect my unfamiliarity with the areas in which these observations were made. As my familiarity with any given area increased, there was a greater probability of seeing the bird when it was not on its log. Nevertheless, the remaining calculations for the activities

Fig. 12. Field maps of the activities of male ruffed grouse in the vicinity of drumming logs. Three males are shown; in addition a map of a "hypothetical male" (6 males combined) is included. All observations were made between 27 April and 1 June, 1968 and 1969.



Male No 7



Male No 913

▲ Blind
t Drumming logs
o Interactions
X Feeding
^ Roosting in trees
• Activity uknown

Male No 906

Hypothetical Male

40 ft

Table 8. Comparison of the activities (average per observation period) of male ruffed grouse at different times of the day and season.

Male No.	Number of observation periods	Total number of hours of observations	Percent of time the whereabouts of the birds were known[a]	Percent of time on each of 5 logs: 1	2	3	4	5	Percent (and number) of times feed
			MORNING EARLY SEASON[c]						
7	5	18	82	67	23	1	-	-	3 (0.8)
906	15	50	84	75	6	6	5	0	4 (0.6)
913	7	31	87	35	29	14	8	-	3 (0.7)
Hypothetical	3	11	34	83	13	-	-	-	0 (0.0)
			EVENING EARLY SEASON[d]						
7	3	9	81	65	31	-	-	-	3 (1.0)
906	12	33	76	98	0	0	0	0	1 (0.2)
913	2	7	70	64	19	5	0	-	3 (1.0)
			MID-DAY EARLY SEASON[e]						
906	1	4	75	100	0	0	0	0	0 (0.0)
913	2	12	48	64	0	26	2	-	1 (1.0)
			MORNING LATE SEASON[f]						
906	12	39	32	48	11	0	20	12	2 (0.3)
Hypothetical	7	23	30	63	23	-	-	-	3 (0.3)
			EVENING LATE SEASON[g]						
Hypothetical	3	9	50	92	0	-	-	-	2 (1.0)

Continued---

Table 8. Continued

Male No.	Percent (and number) of interactions	Percent of other activities[b]	Number of departures from drumming logs
		MORNING EARLY SEASON	
7	0 (0.0)	8	2
906	5 (0.4)	0	3
913	3 (0.7)	8	4
Hypothetical	1 (0.3)	4	1
		EVENING EARLY SEASON	
7	0 (0.0)	0	1
906	2 (0.3)	1	2
913	0 (0.0)	9	3
		MID-DAY EARLY SEASON	
906	0 (0.0)	0	2
913	7 (1.0)	0	1
		MORNING LATE SEASON	
906	2 (0.2)	4	2
Hypothetical	3 (0.3)	7	1
		EVENING LATE SEASON	
Hypothetical	3 (1.7)	4	4

[a]All calculations of activity are based on this time
[b]Time to change logs, or male sighted but activities unknown
[c]0300-0930 hr; 27 April-15 May
[d]1630-2000 hr; 27 April-15 May
[e]0930-1630 hr; 27 April-15 May
[f]0300-0930 hr; 16 May-1 June
[g]1630-2000 hr; 16 May-1 June

of the hypothetical male indicates that the birds making up the hypothetical male were observed sufficiently to accurately document their activity.

The decrease in time that the whereabouts of the birds was known as the day advanced would appear to reflect a decrease in at least some of their activities. Sometimes following an observation period, the area was searched for the birds if they were not in sight from the blind. If found, they were usually seen roosting quietly under spruce. Brander (1965) determined, by using miniature radios on grouse, that the males at least, were inactive from mid-morning until late in the afternoon. The radio-marked birds were usually located under spruce and fir at that time. The decrease in some of the activities of the birds during the mid-day interval is also shown by the decrease in the number of drumming sounds heard (Fig. 4).

Male ruffed grouse spent the greatest proportion of time on their drumming logs during any period. In particular, they appeared to use one log much more than any other. The high proportion of time spent on the logs reflects the amount of drumming done during the reproductive season, and it also may indicate the use of the drumming logs as favoured roosting sites. Even during the mid-day interval when drumming activity was at a relatively low level, male ruffed grouse were seen most often on their logs. The heavy use of logs as roosting sites is not unexpected in view of the secur-

ity afforded by staying on them. Possibly the high use of one log in particular offers the greatest protection, and periodic use of alternate logs may reflect a degree of challenging to adjacent males as indicated in Sec. 6.4.

Male ruffed grouse appeared to be opportunistic in their feeding habits in that no feeding schedules were adhered to. They usually fed as they came to, left, or changed logs.

The time spent involved in interacting with other grouse and the number of interactions were few. This may result from a defence of area by drumming (Sec. 6.4). Nevertheless, from Fig. 12 it can be seen that an area in the vicinity of the logs is defended by actual physical interaction between the resident and an intruder. The tabulation of interactions includes all inter-sexual confrontations. It was difficult to decide whether an intruding grouse was a male or a female, but it appears that both sexes intrude into an area near the logs (Sec. 6.4). Therefore, activities related to actual defence would probably be lower than that shown. It seems that, although an area may be physically defended, this is seldom necessary.

The sizes of the areas seen to be utilized by male ruffed grouse are as follows:

Male No.	Size of area seen to be used (acres)
7	0.43
906	0.80
913	1.20

The mean area is 0.8 acres if the area for the hypothetical male is excluded (0.2 acres). Since this latter is the average of a number of values, it should not be averaged again.

Because males spent the greatest proportion of their time on a single log, most of their activities are grouped around that log. It appears from the observations of behavior and analysis of activity, that in spring the primary log is the focal point of their activities. These activities include all the life functions of the birds: feeding, use of shelter, maintenance activities, and others. This appears to answer an important question first posed by Gullion (1967) about the biology of the species. Are ruffed grouse a lek species? The analysis of dispersion, as well as use of territories for all activities indicates that they are not.

Given that the primary log is the focal point of male ruffed grouse activities in spring, it appears that the field maps may be interpreted as follows. My observations indicated that the males used an area somewhat larger than that shown. For example, often during an interaction the resident male would chase an intruder out of the range of my view from the blind. Nevertheless most of their activities were confined to the depicted areas, particularily in early season. It is suggested that the areas shown represent central cores of concentrated use of larger spaces. Because all life functions seemed to be performed in core areas, the outer cortex of area was probably utilized similarily to the core area. Thus the outer cortex does not represent an area utilized for special functions.

The defense of the areas near the logs indicates that male ruffed grouse are indeed territorial. The points of interaction on the maps represent the points at which the

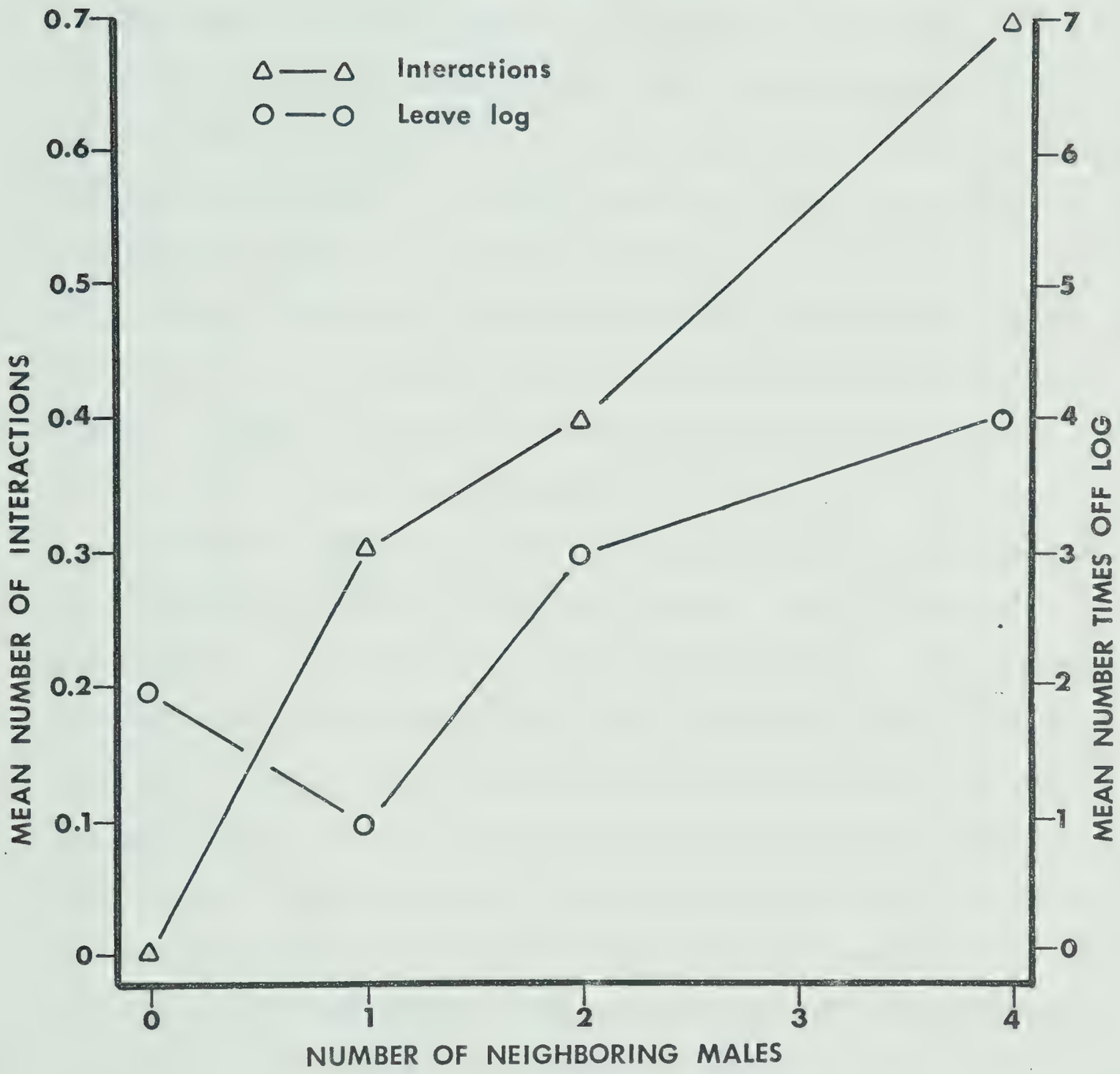
intruders were permitted to approach the log before confronted by the resident. Also, the points of interaction closely follow the boundaries of the spaces outlined.

Territorial activities were more closely examined. The number of adjacent males in a circle with an area of 20 acres was compared to: (1) the average number of times the males left the log; and, (2) the average number of interactions (Fig. 13).

The main purpose for leaving the log was for interactions with other grouse at least during the morning, early season display period, when all display activities were highest. Only this period is considered in the analysis. The results shown indicate a direct relationship between the number of adjacent males and (1) the average number of interactions, and (2) the average number of times the birds left their logs. Therefore activities of adjacent males appear to influence the activities of their neighbors. First, the birds may have left their logs to move to another log in order to challenge a drumming neighbor. The correlation between interactions and number of adjacent males may indicate a degree of territorial boundary formation or maintenance.

Previously it was suggested that at least some of the interactions observed may have been between territorial males and non-territorial males (Sec. 6.4). Thus the relationship between the number of interactions and the number of times a bird left its log versus the density of adjacent males may be due, in part, to the number of non-territorial

Fig. 13. Relationship between density, based on the number of territorial males within a circle of 20 acres centered on each male observed (No. 7, 906, 913, and hypothetical), and the activity (mean number of departures from drumming logs and interactions with other grouse) of the 4 males.


Interactions
Leave log
MEAN NUMBER OF INTERACTIONS
MEAN NUMBER TIMES OFF LOG
NUMBER OF NEIGHBORING MALES
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
7
6
5
4
3
2
1
0
0
1
2
3
4

males, and perhaps females, near the established territories.

Presumably the non-territorial males would tend to select habitat similar to that selected by males that did establish territories. Thus, if there are many territorial males in one area, it would suggest the habitat is optimal. It is expected that non-territorial males may be found in the same general area when they are attempting to establish territories. Similarily, if females come to areas occupied by territorial males for breeding, then one might expect the number of females to be higher where the number of territorial males is higher. Also, females may select habitat similar to that of territorial males as has been indicated in some studies (Berner and Gysel, 1969).

The field maps correspond to the proportion of time that the whereabouts of the birds were known. They represent all sightings for all daily and seasonal periods. The proportion of time the whereabouts of the birds was known varied from 32% (late season) to over 80% (early season). Since the activities of the males were focused around the drumming log(s), the proportion of the activities seen represent the extent of the use of the central core of space. A 68 (100-32) and 20 (100-80)% use of an outer cortex of space was calculated. From each blind location an area greater than that shown to be used by each male could be seen, but no birds were sighted within this area. This may have resulted from two different factors. First, in early season, the birds did not use this space very much. Secondly, in late season

when attendance on the logs had decreased, it was difficult to sight the birds from the blinds if the birds were not first seen on their logs and watched when they left. Thus the size of territories indicated (mean of 0.6 acres) represents a minimum area.

Measurements between centers of territories in areas of greatest density gave an average area of 1.4 acres per territory (Sec. 7.1). It was suggested that this area may represent the actual average minimum territory size. If this is so, then size of territories indicated on the field maps may only be about 50% of the actual minimum territory size. Male No. 913, the most active bird, as judged from the number of interactions and number of times the bird left the log, used an area of 1.2 acres. It seems likely then that the average minimum size territory in ruffed grouse may be about one acre. Fowle (1953) has shown that the size of territory of ruffed grouse may vary with population density. He determined that the size of territories used varied from about 0.9 to 2.2 acres. The lower value agrees closely with that estimated in the present study as the minimum territory size.

To sum up, it would appear that in early season at least male ruffed grouse make heavy use of an area near their logs. From this area of concentrated use the males move outwards to approach other ruffed grouse and investigate any grouse-like sounds. It is likely also that even in the absence of penetration of other ruffed grouse into an occupied territory,

the resident would make periodic forays away from the drumming logs. This appeared to be true since I was often unable to locate the male near the logs. I do not suggest in this latter instance that the boundaries of territories are patrolled. This seems unlikely in view of the large proportion of time spent on the drumming logs. Rather, it would seem that aside from the core area near the logs where advertisement (drumming) is greatest, some additional time is spent away from the core areas shown in Fig. 12.

Studies in other populations of ruffed grouse have shown that the area utilized by male ruffed grouse increases from spring, through summer to fall (Eng, 1959; Fowle, 1953). Reasons for increased mobility are unknown, but I suggest that this may reflect a gradual gonadal regression which would make attachment to the drumming log weaker. It seems that such attachment is closely linked with reproductive events and hence with early season use of the logs (Sec. 5.1). In this view, the low proportion of time that the whereabouts of the males were known in late season may be explained by a weakened attachment to logs.

Fowle (1953) has shown that the areas utilized by male ruffed grouse in spring do not overlap. It was not possible in the present study to determine if the areas utilized in spring overlapped. However, if they did, my observations indicate that the grouse rarely came into contact, at least in early season, since they spent such a large proportion of time on their logs. In late season there was possibly some overlap since much less time was spent in the vicinity

of the drumming logs. This may not be unexpected since drumming activity and reproductive events were at a very low level at that time (Fig. 3). In other words, territoriality appeared wane to a very low level.

After a brief period in fall of increased attachment to the drumming logs and coincident drumming activity (Sec. 5.2) the area utilized by male ruffed grouse is greatly extended outwards from their logs (Eng, 1959; Fowle, 1953). This, and the evidence for some winter flocking (Bump et al., 1947) suggests that areas utilized by male ruffed grouse in all seasons except spring, and possibly fall, are best thought of as home ranges. Territories do not appear to be separate from the home ranges, but rather are small, defended portions within them.

Since an area near the drumming logs is defended, then male ruffed grouse are territorial in spring. Territorial activity wanes as the seasons advance. These results suggest that the term "territory" and "home range" are adequate to describe the areas utilized. The terms "activity center" and "primary area" appear to be irrelevant and unnecessary.

7.3 Age Composition of Drumming Males

Sumanik (1966) used a method devised by Wishart (*unpubl.*) and based on the greatest diameter of the rachis at the superior umbilicus to distinguish yearling from adult male ruffed grouse. The same method was used to determine

the ages of territorial male ruffed grouse caught subsequently on the same study areas.

The age ratio of territorial males in the population removed from the West Area in 1965 was 2.6 yearlings to 1.0 adult. Five territories were reoccupied by different males that spring after removal and all the reoccupants were yearlings. In 1966 ten territorial males were caught on the West Area and all of these were yearlings. These data, and those of Dorney and Kabat (1960) obtained in Wisconsin show that there is no surplus of non-territorial adults, but there may be a surplus of yearling males. Since the same results show that some yearling, non-territorial males take up territories with the removal of the territorial cohort, then it would appear that some yearlings are prevented from holding territories. Since the number of physical interactions between ruffed grouse is low, then some other mechanism may be used by territorial males that prevent some yearlings from holding territories. It is suggested that drumming may serve this function since it is the only loud and directional sound produced by territorial males.

Before the implications of the suggestion that some male ruffed grouse are prevented from holding territories can be properly assessed, more information is required. For example, in all years the number of non-territorial yearling males was unknown. Whether this number fluctuates between years is also unknown. Further, in blue grouse it

has been shown that a proportion of yearling males were physiologically immature and did not take up territories even after removal of the territorial population (Bendell and Elliot, 1967). This may be also true of ruffed grouse.

7.4 Functions of Territory in Ruffed Grouse

Male ruffed grouse defend a small area in the vicinity of their logs. Because the males spent such a large proportion of their time on or near their drumming logs it is unlikely that a habitat resource was being defended. Food does not appear to be a prime requisite for the establishment of a territory. Neither does protection from predation since logs are only slightly used in summer and winter, and defence is not seen at these times. Intruding ruffed grouse are permitted to closely approach the territorial male. If some habitat commodity was being defended, it seems a larger area than that observed would be defended. This would be true unless the "commodity" was only sufficient in a small area. However, at present what this could be is unknown.

That male ruffed grouse form and defend territories primarily during the breeding season suggests that the function of territory is concerned with reproduction.

The males are largely localized to small areas during the reproductive season, whereas hens are much more mobile (Hale and Dorney, 1963). This information suggests that the primary function of territorialism in ruffed grouse is to

bring the sexes together for mating. Since male ruffed grouse have no role in nest site selection, incubation, or care of the young (Bump et al., 1947) it would appear that territorialism may be concerned only with the actual mating process.

However, if localization to a small area does aid in bringing the sexes together, defen e of that space is still not explained. Why are isolated (territorial) males aggressive towards one another? This can be explained by postulating an original competition for mates. In this view, through evolution the males isolated themselves through aggression and now advertise themselves to females, presumably by drumming. Also, the level of drumming activity may be a reflection of the aggressiveness of the males. Thus the most aggressive males may be the most successful in obtaining mates since, while on their territories they are free from dispossession and maintain a high level of advertisement to females. Furthermore, because of the isolation achieved through territorial activity, it is likely that interference with mating is reduced. Armstrong (1942) gives many examples of this phenomenon.

It is possible that subsidiary benefits accrue from the territorial system. Thus, drumming may not only aid the females in finding males, but may also serve to stimulate receptivity in the females.

Other benefits of the system may have survival value for the cocks. For example, familiarity with a small area may aid the territorial males in escaping predators, as shown in other birds (Tinbergen, 1957). Range extension through dis-

persal of non-established birds excluded by aggression of territorial males from blocks of habitat may be another advantage of such a system.

One basic theoretical question asked at the start of this paper was whether territorialism should be considered as a behavioral phenomenon rather than a spatial one. In ruffed grouse, it seems apparent that territorialism is primarily a behavioral phenomenon, although secondary ecological benefits may be derived from the system.

8. CONCLUDING DISCUSSION

The function of territory in ruffed grouse appears to be primarily related to reproduction. However, an understanding of the reproductive system is incomplete. Data presented indicate that male ruffed grouse live and display alone. Territories are presumably mating areas. However, how many territorial males breed is unknown. Does one male perform most matings, or do a number of males contribute? Since adjacent territorial males influence the activities of their neighbors, one wonders if there is a hierarchial (dominance) system amongst males.

Tests of dispersion indicate that established territorial males do not influence non-territorial males to ultimately settle near them, or that territories are successively reused. But since the population was expanding, it was difficult to decide what some of the factors influencing dispersion were. In a stable population it would seem easier to determine the pattern of use of territories.

If one or a few males perform most matings and a tradition of use of adjacent territories could be demonstrated, then one could argue that ruffed grouse are a lek, or incipient lek species. In this view, territories are primarily display grounds, as seems to be the case, and groups of males come to their logs together to perform their displays. There is some evidence for this latter suggestion. Then

females seek out particular males with which to mate. However, information about the behavior of the hens in the field is almost completely lacking.

To answer some of the questions about the mating system in ruffed grouse would require monitoring the behavior of a number of males simultaneously and the activity of hens. Possibly the only way to do this would be with miniture radios, although at present not enough is known about the influence of radios on these birds.

Much further work can be done with an analysis of behavior patterns in ruffed grouse. In particular, more work is needed for an understanding of courtship, and this again illustrates the lack of knowledge about the reproductive system.

In summary, with the present data, the conservative view is that male ruffed grouse live and display alone, and that each drumming male has an equal chance of attracting and mating with one or more hens.

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Appendix 1. Example of a data sheet used to map movements of grouse. This particular map was used to mark the locations of male No. 906 in 1969.

DATE _____

TIME _____ TO _____

BIRDS _____ _____ _____

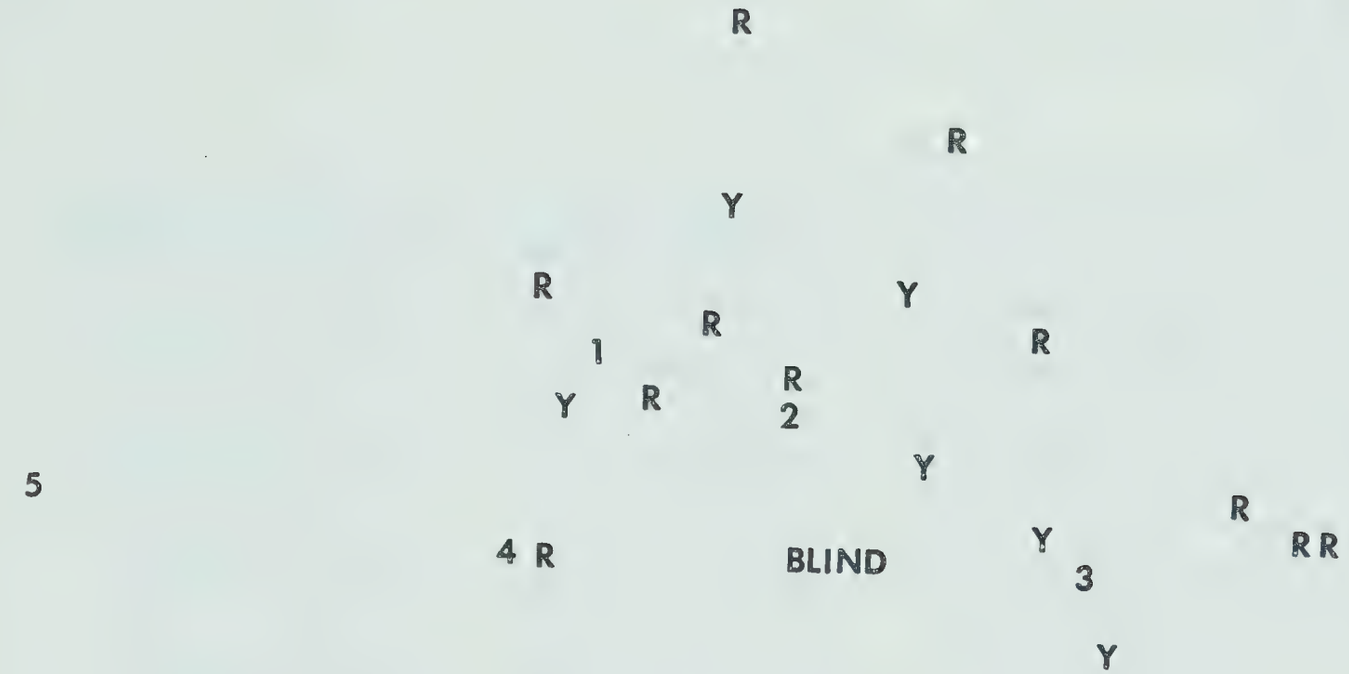
AREA - TERRITORY OF MALE NO. 906

PAGE _____

SCALE - 1 cm = 25'

R, Y: Red and yellow strips of surveyors tape tied to trees.

Nos. 1 - 6: Drumming logs.



Appendix 2. Time intervals between thumps (in seconds) of the drumming sequences of 7 male ruffed grouse recorded in southwestern Alberta, 1969. Time intervals are read sequentially from left to right and top to bottom.

Male No.	Number of thumps in each sequence	Intervals between thumps
906	46	0.38 0.46 0.52 1.00 0.88 0.72 0.58 0.48 0.42 0.38 0.32 0.30 0.28 0.24 0.22 0.20 0.18 0.16 0.14 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.08 0.08 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12
	46	0.38 0.46 0.52 1.02 0.88 0.70 0.56 0.48 0.42 0.36 0.32 0.30 0.26 0.24 0.22 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.12 0.12 0.14
	47	0.38 0.46 0.52 1.00 0.86 0.70 0.56 0.48 0.42 0.36 0.32 0.30 0.26 0.24 0.22 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.12 0.16 0.16

Appendix 2. Continued

Male No.	Number of thumps in each sequence	Intervals between thumps
906	45	0.38 0.46 0.52 1.00 0.88 0.72 0.58 0.48 0.42 0.36 0.32 0.28 0.26 0.24 0.22 0.20 0.18 0.16 0.14 0.14 0.12 0.12 0.11 0.16 0.11 0.11 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.14
16	49	0.34 0.48 0.54 1.02 0.84 0.60 0.58 0.48 0.42 0.36 0.32 0.30 0.26 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.12 0.12 0.12 0.14
	49	0.34 0.48 0.56 1.02 0.82 0.68 0.58 0.48 0.42 0.38 0.34 0.30 0.26 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.12 0.12 0.14
	49	0.34 0.48 0.54 1.00 0.82 0.70 0.58 0.48 0.40 0.38 0.32 0.30 0.28 0.24 0.22 0.20 0.18 0.18 0.16 0.16 0.14 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.12 0.12 0.12 0.14

Appendix 2. Continued

Male No.	Number of thumps in each sequence	Intervals between thumps
16	49	0.34 0.48 0.56 1.02 0.84 0.68 0.58 0.48 0.42 0.38 0.32 0.30 0.26 0.24 0.22 0.20 0.18 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.08 0.06 0.06 0.04 0.04 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.12 0.14
?	48	0.34 0.44 0.52 1.00 0.86 0.72 0.62 0.52 0.46 0.40 0.34 0.32 0.28 0.26 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.08 0.08 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.10 0.10 0.10 0.12 0.14 0.16 0.16
	48	0.34 0.44 0.52 0.98 0.86 0.72 0.62 0.52 0.46 0.38 0.36 0.30 0.28 0.26 0.22 0.20 0.20 0.18 0.16 0.16 0.14 0.12 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.14
	48	0.34 0.44 0.54 0.98 0.86 0.72 0.62 0.52 0.44 0.40 0.34 0.30 0.28 0.26 0.22 0.20 0.20 0.18 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.08 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.06 0.08 0.08 0.10 0.10 0.11 0.12 0.12 0.14

Appendix 2. Continued

Male No.	Number of thumps in each sequence	Intervals between thumps
?	48	0.34 0.44 0.54 1.00 0.84 0.72 0.80 0.50 0.46 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.16
688	47	0.36 0.40 0.46 0.86 0.84 0.70 0.58 0.48 0.42 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.14
	47	0.36 0.40 0.46 0.84 0.84 0.68 0.56 0.48 0.42 0.38 0.36 0.34 0.26 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.14
	47	0.36 0.40 0.46 0.84 0.82 0.68 0.56 0.48 0.42 0.38 0.34 0.30 0.26 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.06 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.14

Appendix 2. Continued

Male No.	Number of thumps in each sequence	Intervals between thumps
688	47	0.36 0.40 0.46 0.66 0.82 0.68 0.56 0.48 0.42 0.38 0.34 0.30 0.26 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.06 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.14 0.14
	47	0.36 0.40 0.46 0.86 0.82 0.68 0.58 0.48 0.42 0.38 0.34 0.30 0.26 0.24 0.22 0.20 0.20 0.18 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.14
	47	0.36 0.40 0.48 0.88 0.84 0.70 0.58 0.50 0.42 0.36 0.34 0.30 0.26 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.06 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.14
905	45	0.38 0.48 0.52 1.04 0.80 0.62 0.58 0.50 0.42 0.38 0.34 0.30 0.28 0.26 0.22 0.20 0.18 0.16 0.16 0.16 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.06 0.08 0.04 0.06 0.06 0.06 0.08 0.10 0.10 0.10 0.10 0.10 0.12 0.14 0.14 0.16

Appendix 2. Continued

Male No.	Number of thumps in each sequence	Intervals between thumps
905	45	0.38 0.46 0.52 1.02 0.80 0.70 0.58 0.50 0.44 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.06 0.06 0.04 0.04 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.14 0.14 0.16
	44	0.38 0.46 0.54 1.02 0.80 0.68 0.58 0.50 0.42 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.20 0.18 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.08 0.10 0.10 0.11 0.10 0.12 0.12 0.12 0.16
	45	0.38 0.48 0.52 1.02 0.80 0.70 0.58 0.50 0.44 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.14 0.14 0.16
	44	0.38 0.46 0.52 1.04 0.82 0.70 0.58 0.50 0.42 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.11 0.10 0.10 0.08 0.08 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.14 0.14

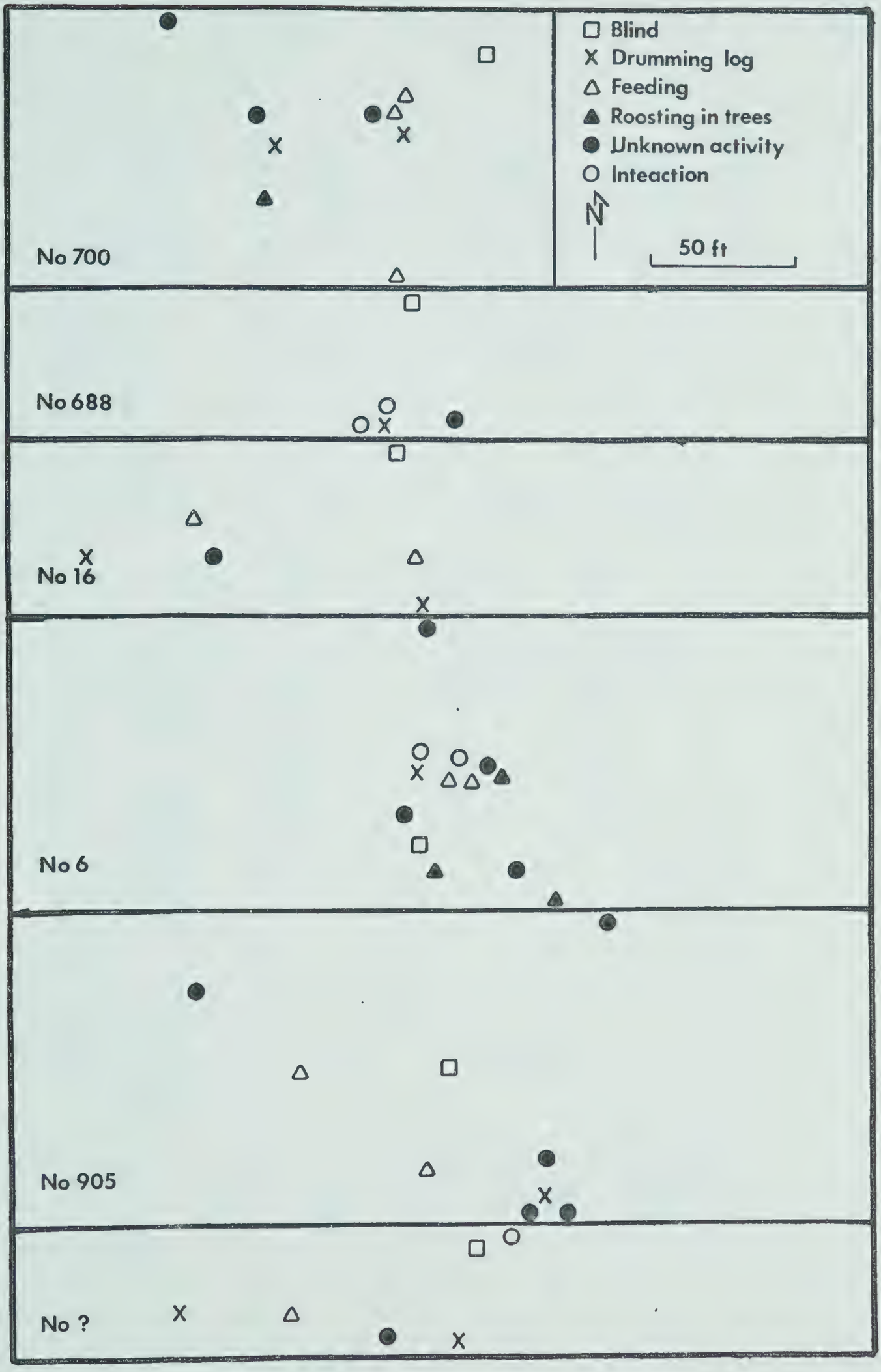
Appendix 2. Continued

Male No.	Number of thumps in each sequence	Intervals between thumps
700	47	0.38 0.46 0.52 1.00 0.84 0.72 0.60 0.50 0.44 0.40 0.34 0.32 0.28 0.26 0.24 0.20 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.12 0.11 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.06 0.06 0.06 0.08 0.0 0.08 0.08 0.10 0.10 0.11 0.12 0.12 0.1
	47	0.38 0.46 0.52 1.00 0.88 0.77 0.60 0.52 0.44 0.40 0.36 0.32 0.28 0.26 0.24 0.20 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.12 0.12 0.12
	47	0.38 0.46 0.52 1.00 0.84 0.72 0.60 0.60 0.44 0.40 0.34 0.32 0.28 0.26 0.24 0.20 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.12 0.12
	48	0.38 0.46 0.52 1.02 0.86 0.72 0.60 0.52 0.44 0.40 0.36 0.30 0.28 0.26 0.24 0.20 0.20 0.18 0.16 0.14 0.14 0.14 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.08 0.08 0.10 0.10 0.10 0.10 0.10 0.12 0.12 0.14

Appendix 2. Continued

Male No.	Number of thumps in each sequence	Intervals between thumps
6	48	0.36 0.44 0.46 1.08 0.86 0.77 0.60 0.50 0.42 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.12 0.12
	47	0.36 0.44 0.46 1.08 0.86 0.72 0.62 0.50 0.44 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.12 0.12 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.06 0.04 0.06 0.06 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.12
	49	0.36 0.44 0.46 1.08 0.86 0.74 0.62 0.52 0.44 0.38 0.34 0.30 0.28 0.24 0.22 0.20 0.18 0.18 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.04 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.12 0.12 0.14
	48	0.34 0.42 0.46 1.06 0.84 0.72 0.60 0.50 0.44 0.38 0.34 0.30 0.26 0.24 0.22 0.20 0.18 0.16 0.16 0.14 0.14 0.12 0.12 0.10 0.10 0.10 0.08 0.08 0.08 0.06 0.06 0.04 0.04 0.06 0.06 0.06 0.08 0.08 0.08 0.08 0.08 0.10 0.10 0.10 0.10 0.10 0.12

Appendix 3. Field maps and analysis of the activities of male ruffed grouse in the vicinity of drumming logs. These data were used to make up the hypothetical male. Data were obtained between 27 April and 1 June, 1969.


Blind
Drumming log
Feeding
Roosting in trees
Unknown activity
Inteaction
N
50 ft
No 700
No 688
No 16
No 6
No 905
No ?

Appendix 3. Comparison of the activities (average per observation period) of male ruffed grouse at different times of the day and season.

Male No.	Number of observation periods	Total number of hours of observations	Percent of time the whereabouts of the birds were known[1]	Percent of time on each of 2 logs		Percent (and number) of times feed
				1	2	
			MORNING EARLY SEASON[a]			
905	1	4	75	99	-	0 (0.0)
?	2	7	11	30	62	0 (0.0)
			MORNING LATE SEASON[b]			
6	2	7	24	75	0	0 (0.0)
16	1	2	100	46	43	5 (1.0)
688	2	7	33	85	10	0 (0.0)
700	2	7	18	54	36	4 (0.5)
			EVENING LATE SEASON[c]			
6	1	3	56	84	-	3 (1.0)
688	1	3	31	100	0	0 (0.0)
700	1	3	100	96	0	4 (2.0)

Continued---

Appendix 3. Continued

Male No.	Percent (and number) of interactions	Percent of other activities[2]	Number of departures from drumming logs
		MORNING EARLY SEASON	
905	0 (0.0)	1	2
?	0 (0.0)	8	0
		MORNING LATE SEASON	
6	8 (1.0)	17	2
16	0 (0.0)	9	3
688	4 (1.0)	0	1
700	0 (0.0)	6	2
		EVENING LATE SEASON	
6	6 (2.0)	13	5
688	5 (1.0)	0	0
700	2 (2.0)	0	1

[a]0300-0930 hr; 27 April-15 May

[b]0300-0930 hr; 16 May-1 June

[c]1630-2000 hr; 16 May-1 June

[1]All calculations of activity are based on this time.

[2]Time to change logs, or male sighted but activities unknown